POLAR BEAR (*URSUS MARITIMUS*) FORAGING ECOLOGY IN THE WESTERN CANADIAN ARCTIC

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Abstract

Climate change has led to abrupt declines in sea ice over the past three decades. Polar bears (*Ursus maritimus*) rely on sea ice as their primary habitat to hunt marine mammal prey. Due to their position at the top of the Arctic marine food web, polar bear foraging patterns can provide insights on ecosystem structure and function both spatially and temporally. This thesis used quantitative fatty acid signature analysis (QFASA) to estimate the diets, and adipose tissue lipid content to estimate the body condition, of polar bears in three western Canadian Arctic subpopulations: Northern Beaufort Sea, Southern Beaufort Sea, and Viscount Melville Sound. This thesis identified spatial, temporal, and intraspecific variation in the relationships between sea ice conditions, and polar bear diet and body condition. Polar bears with the greatest ecological constraints on diet composition may be most vulnerable to climate-related changes in ice conditions and prey availability.

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Chapter 1: Introduction

Background Information

Food Web Ecology

Food webs are defined as the flow of energy from primary producers, through consumers, to apex predators (Elton 1927). Food webs can be classified into groups of organisms in discrete trophic levels, where links between the levels represent the flow of energy within a system (Lindeman 1942). Species at higher trophic levels forage on species at lower tropic levels, which indirectly and directly affects species at all levels of the food web in an ecosystem (Steele 1974; Schmitz and Suttle 2001). Bottom-up systems are controlled by low trophic level species, where an increase in primary productivity results in greater productivity throughout the food web, and top-down systems occur when the consumption by a higher trophic level species depresses the trophic level that they are feeding on, in turn increasing the productivity next trophic level below (Hairston et al. 1960). In both systems, ecosystem change can often be reflected in apex predator ecology, such as movement, distribution, abundance, body condition, and foraging (Paine 1966; Bowen 1997; Wilmers and Getz 2005; Hazen et al. 2012). The relative rate of ecosystem change is important to consider when analyzing effects at both the population and ecosystem level.

Climate Change

Rapid declines in sea ice thickness (Lindsay and Schweiger 2015), extent (Stroeve et al. 2012), and seasonal duration (Wang and Overland 2015) are occurring throughout the circumpolar Arctic. Declines are occurring at a greater than forecasted rate, and are projected to accelerate on a global scale (Stroeve et al. 2012). Polar bears are dependent on sea ice as a platform for hunting, travelling, and mating (Amstrup 2003), and changes in sea ice conditions have been

linked to declines in polar bear body condition (Stirling et al. 1999; Rode et al. 2010, 2012; Obbard et al. 2016), reproduction (Regehr et al. 2007; Rode et al. 2010), and survival (Regehr et al. 2007; Peacock et al. 2012; Bromaghin et al. 2015). Variation in the population-level consequences of sea ice decline in different regions may reflect the complex effects of climate change on different spatial and temporal scales (Rode et al. 2014; Rogers et al. 2015). Information on polar bear foraging ecology is critical for understanding and forecasting Arctic marine ecology in a changing climate.

Polar Bear Ecology

The Polar Bear Specialist Group (PBSG) of the International Union for the Conservation of Nature (IUCN) recognizes 19 relatively discrete subpopulations of polar bears worldwide (Fig. 1.1; Obbard et al. 2010) based on telemetry data, traditional knowledge, and ecological life history (Aars et al. 2006). Bears in different subpopulations often experience different environmental conditions and show various life history strategies. Four different Arctic ecoregions can be identified based on predominant sea ice regimes (Amstrup et al. 2008): *divergent ice* on the coast of Alaska and Russia, *convergent ice* on the northwest and northern edge of the Canadian Archipelago through eastern Greenland, the *archipelago* within Canadian Archipelago, and *seasonal ice* in Baffin Bay, Davis Straight, Foxe Basin and Hudson Bay. The divergent ice ecoregion (e.g., Southern Beaufort Sea subpopulation) experiences ice forming along the shore that retreats during the summer months, forcing polar bears to choose to stay ashore until the ice returns in the fall, or remain on the offshore pack ice where productivity is not high, and prey species may or may not be present. In the convergent ice ecoregion (e.g., Northern Beaufort Sea subpopulation) ice from other areas in the Arctic accumulates along the shoreline providing polar bears access to seals. Where monitoring has taken place, polar bear

populations in these subpopulations are considered stable. In the archipelago ice ecoregions (e.g., Viscount Melville Sound subpopulation) heavy annual (and historically multiyear) ice fills the interisland channels throughout the year, providing a hunting platform and access to seals. Some subpopulations, such as the Viscount Melville Sound subpopulation, have not been studied recently and are poorly understood. In the seasonal ice ecoregion (e.g., Western Hudson Bay subpopulation) polar bears come ashore for several months when the seasonal sea ice melts completely each summer, and rely on stored energy (fat) while waiting for the ice to refreeze again in the fall (Stirling et al. 1999).

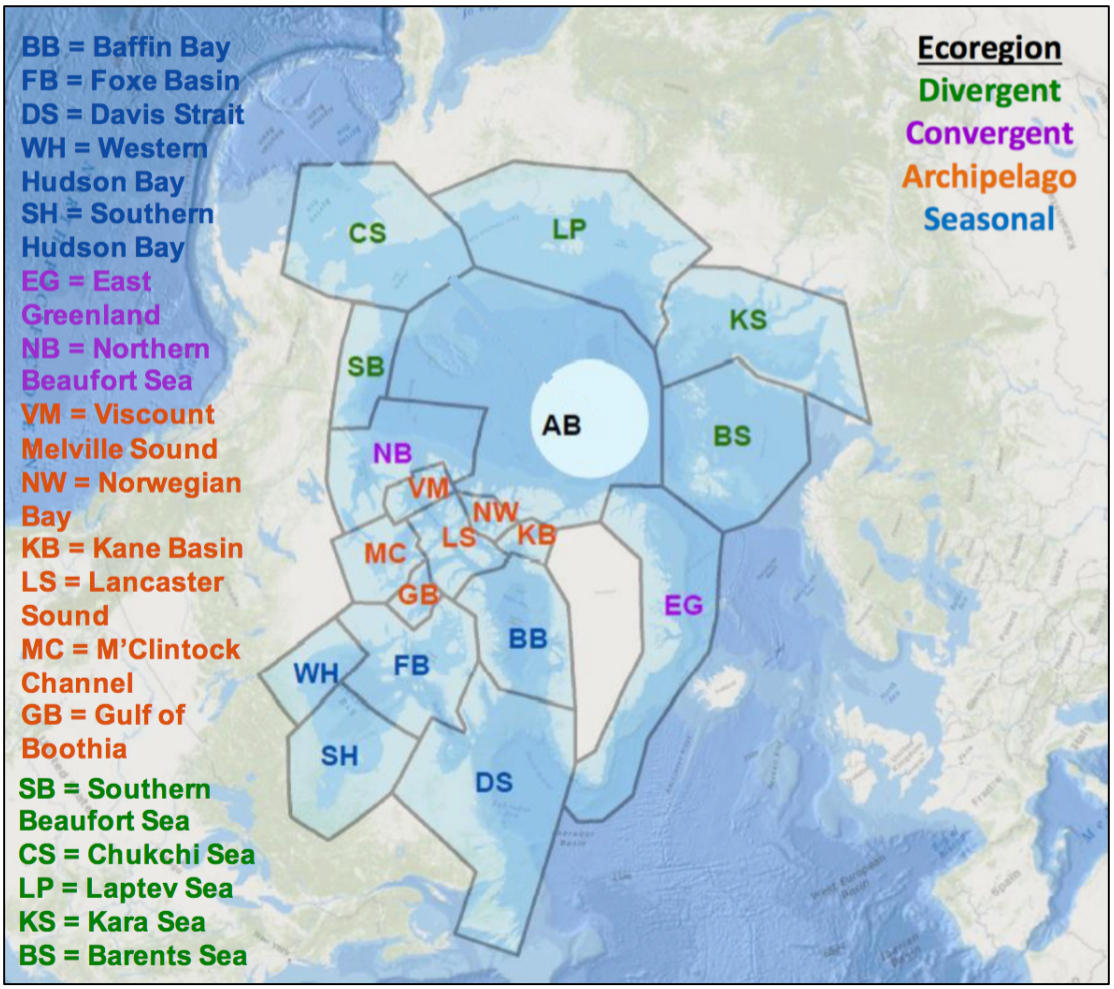

Figure 1. 1 Circumpolar distribution of the 19 polar bear subpopulations.

Polar Bear Diet

Local sea ice conditions may be a primary determinant of polar bear foraging success (Stirling and Derocher 2012; Pilfold et al. 2015). Polar bears may be considered opportunistic foragers, that is, they will hunt or scavenge on locally abundant and accessible prey sources (Smith 1980; Lowry et al. 1987; Smith and Sjare 1990). Polar bear diet composition may differ across age and sex, due to differences in hunting ability, energetic requirements, and reproductive ecology. Adult males are roughly twice the size of adult females, allowing males to hunt larger-bodied prey (Derocher et al. 2005, 2010). Throughout their circumpolar range, polar bears primarily feed on ringed seals (Thiemann et al. 2008). Ringed seals are a small bodied prey that are accessible by bears of most age classes and both sexes (Kingsley et al. 1985). However, ringed seals are an ice-dependent species, where in the winter pregnant females dig out birth lairs in a snowdrift above a breathing hole maintained in the ice (Smith and Stirling 1975). Ringed seals give birth to their pups in these lairs, which provide protection from predators and thermoregulatory benefits (Smith and Stirling 1975). The pups remain in the lair for approximately six weeks while gaining body fat from their mother's milk. The latter stage of the pupping season represents a key time of year for polar bears, as the newly weaned pups are inexperienced with predators and are approximately 50% body fat, providing an excellent source of blubber for polar bears. Ringed seals rely on suitable snow and ice conditions for the construction of birth lairs and successful reproduction (Ferguson et al. 2005). As such, ringed seals are vulnerable to abrupt climatic changes (Ferguson et al. 2005; Ferguson and Anderson 2016; Yurkowski et al. 2016), and declines in ringed seal natality will affect polar bear reproductive success and survival (Stirling 2002). Polar bears also feed on locally available prey, including bearded seals (*Erignathus barbatus;* Thiemann et al. 2007, 2008), harp seals

(*Pagophilus groenlandica;* Derocher et al. 2002; Galicia et al. 2015), harbour seals (*Phoca vitulina;* Thiemann et al. 2008; Sciullo et al. in press), walrus (*Odobenus rosmarus;* Calvert and Stirling 1989; Thiemann et al. 2007) beluga whales (*Delphinapterus leucas;* Freeman 1973), narwhals (*Monodon monoceros;* Smith and Sjare 1990), and the carcasses of bowhead whales (*Balaena mysticetus;* Herreman and Peacock 2013).

Diet Analyses

Several methods have been used for analysis of predator diet, including stomach contents, prey remains (e.g., Elbroch and Wittmer 2013), and predator scat analysis (i.e., Du Preez et al. 2017). These methods have been used in the analysis of polar bear diet in the past (i.e., Stirling and Archibald 1977; Smith 1980; Smith and Sjare 1990). Unfortunately, these methods of diet analysis typically provide only a snapshot of the predator's most recent meal and may not accurately reflect diet over ecologically relevant timescales. With more detailed information on a predator's diet over several weeks or months, we can more accurately understand the relationship between predators, prey, and their environment.

Lipids and Fatty Acids

Lipids are compounds that are soluble in organic solvents (i.e., chloroform, hydrocarbons, alcohols) but not water (Budge et al. 2006). Most lipids are primarily composted of fatty acids (FA), which are made up a straight or branched chain of carbons with a methyl group on one end, and carboxyl group on the other end. FA are expressed by the shorthand nomenclature of *A:B*n-*X,* where *A* is the length of the carbon chain (usually even numbers from 12-24), *B* is the number of double bonds (0-6), and *X* is the position of the first bond relative to the terminal methyl group (Iverson et al. 2004; Budge et al. 2006). FA can be classified into groups based on the number of double bonds or location of a methyl branch. Straight-chained FA are classified as

a *saturated FA* if it has zero double bonds, a *monounsaturated FA* if it has one double bond, or a *polyunsaturated FA* if it has two or more double bonds. Branched FA are classified as a FA with *iso* (abbreviated: *i*) as a prefix if it has a methyl branch at the second carbon, and a FA with an *anti-iso* (abbreviated: a*i*) prefix if it has a methyl branch at the third carbon (Iverson et al. 2004; Budge et al. 2006).

The relative abundance of multiple FA in the adipose stores of an animal (referred to as its FA profile or signature) is a function of both diet and endogenous processes. Dietary FA are predictably incorporated into a predator's fat stores with little or no modification, unlike proteins and carbohydrates (Ackman and Eaton 1966; Iverson et al. 2004). The distinct FA signatures of different prey, and the limited synthesis of FA in the consumer allows FA analysis to provide insights into a predator's diet over weeks to months before the sample was obtained (Brockerhoff et al. 1967; Iverson et al. 2004).

Polar bears primarily use superficial (subcutaneous) adipose tissue for lipid energy storage (Pond 1992). Thus, the FA composition of a bear's subcutaneous fat should provide insights into its recent diet. Moreover, as polar bears store and mobilize lipids, the proportion of lipid to non-lipid components in their adipose tissue increases and decreases, respectively (Pond 1992). The proportion of lipid in adipose tissue has served as an indicator of body condition in polar bears (Thiemann et al. 2006; Stirling et al. 2008; McKinney et al. 2014; Sciullo et al. 2016).

Quantitative Fatty Acid Signature Analyses

The quantitative fatty acid signature analysis (QFASA) model (Iverson et al. 2004) is a multivariate least squares model that uses the FA signatures of a predator and its potential prey to generate estimates of predator diet. After accounting for FA-specific patterns of metabolism in

the predator, the QFASA model determines the proportional combination of prey signatures that comes closest to matching the observed predator. QFASA has been previously used to estimate the diet composition of polar bears across the Canadian Arctic (Thiemann et al. 2008), and in specific subpopulations (Rode et al. 2014; Galicia et al. 2015, 2016; McKinney et al. 2017).

Thesis Organization and Research Objectives

This thesis is formatted as two independent manuscripts (*Chapter 2* and *Chapter 3*) with an overall introduction of background information (*Chapter 1*) and discussion of my main findings and conclusions (*Chapter 4*).

Chapter 2 examines the diet composition and body condition of polar bears using adipose tissue samples from bears harvested in the Northern Beaufort Sea (NB) and Southern Beaufort Sea (SB) from 1999 to 2015. The Beaufort Sea analyses will examine polar bear diet composition during a period of rapid sea ice loss and demographic decline in the SB subpopulation. A recent study by Bromaghin et al. (2015) suggested that reduced prey availability and sea ice declines in SB have led to a decline in the survival and abundance of bears since 2004. This chapter examines the spatial, temporal, seasonal, and age- and sex-specific trends in diet and body condition, in relation to sea ice conditions, which provides insights into the decline in survival and abundance of bears during the study period.

Chapter 3 aims to quantify the diet composition and body condition of polar bears in the Viscount Melville Sound subpopulation from mark-recapture studies from 2012-2014. The foraging habits of bears in this subpopulation have never been examined, and much of the ecology of this region is poorly understood. As such, this chapter will analyze sea ice trends that may be driving foraging patterns of polar bears as important baseline dietary information.

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Chapter 2: Drivers and consequences of polar bear (*Ursus maritimus*) diet composition in the Canadian Beaufort Sea

Abstract

Polar bears (*Ursus maritimus*) rely on annual sea ice as their primary habitat for hunting marine mammal prey. Given their long life span, wide geographic distribution, and position at the top of the Arctic marine food web, the diet composition of polar bears can provide insights into the temporal and spatial ecosystem dynamics related to climate-mediated sea ice loss. Polar bears with the greatest ecological constraints on diet composition may be most vulnerable to climate-related changes in ice conditions and prey availability. I used quantitative fatty acid signature analysis (QFASA) to estimate the diets of polar bears in two western Canadian Arctic subpopulations: Northern Beaufort Sea (NB) and Southern Beaufort Sea (SB), areas where sea ice conditions have declined in the past 30 years. Polar bear diets were dominated by ringed seal (*Pusa hispida*), with interannual, seasonal, age- and sex- specific variation. Location and sea ice conditions also affected polar bear diet composition. Most variation in bear diet was explained by longitude, with adult males along the western coast of Banks Island and near the Tuktoyaktuk Peninsula relying heavily on bearded seal (*Erignathus barbatus*). Sea ice conditions declined throughout the study period, and date of sea-ice break-up was positively correlated with adult female consumption of beluga whale (*Delphinapterus leucas*) and body condition, perhaps suggesting polar bears foraged on beluga whales during entrapment events. Adult female body condition was positively correlated with ringed seal consumption, and adult male body condition was negatively correlated with beluga whale consumption. This study provides insights into the complex relationship between sea ice conditions and polar bear diet composition and foraging success.

Introduction

Climate warming has contributed to rapid declines in sea-ice extent, thickness, and seasonal duration in the Arctic (Maslanik et al. 2011; Stroeve et al. 2012; Lindsay and Schweiger 2015). Global climate models have shown greater-than-forecasted declines in sea-ice, and these declines are projected to accelerate and continue through 2100 (Stroeve and Notz 2015; Wang and Overland 2015). Although changes in sea-ice metrics are well documented, the ecological consequences are more difficult to assess and likely vary by region and over time (Wassmann et al. 2011; Stern and Laidre 2016).

The response of a species to environmental change is often predicted by the relationship of the organism with its habitat (Parmesan 2006). Apex predators are top trophic-level organisms that influence the ecology of food webs (Katona and Whitehead 1988; Horswill et al. 2016) and can serve as indicators of ecosystem change (Bowen 1997). Polar bears (*Ursus maritimus*) are apex predators with a wide geographical range, a long lifespan, and may be particularly sensitive to climate-induced ecosystem change due to their reliance on sea-ice as a platform for hunting, travelling, and mating (Stirling and Derocher 1993; Durner et al. 2017; Lone et al. 2017; Togunov et al. 2017). Long-term changes in sea ice conditions have been associated with declines in polar bear body condition (Stirling et al. 1999; Rode et al. 2010; Obbard et al. 2016), reproduction (Regehr et al. 2007; Rode et al. 2010), survival (Regehr et al. 2007; Peacock et al. 2012) and abundance (Regehr et al. 2007; Bromaghin et al. 2015; Lunn et al. 2016). The effects of declining sea ice on polar bear demography are expected to be primarily mediated by changes in prey availability (i.e., spatio-temporal distribution and abundance) leading to reduced foraging opportunities for polar bears.

Polar bears feed on a variety of marine mammal species throughout their range (Derocher et al. 2002; Thiemann et al. 2008a). Studies suggest polar bears feed primarily on ringed seals (*Pusa hispida*; Thiemann et al. 2008a), which have a wide distribution and high abundance throughout the Canadian Arctic (Kingsley et al. 1985). Polar bears of most age classes and both sexes are able to hunt ringed seals as they are the smallest Arctic seal species (Kingsley et al. 1985). However, ringed seals are dependent on sea-ice and snow for resting, molting, and building lairs above breathing holes where they retreat to rear their pups (Smith and Stirling 1975), which may make them vulnerable to abrupt climatic changes (Ferguson et al. 2005, 2017; Ferguson and Higdon 2006; Chambellant et al. 2012; Yurkowski et al. 2016a). During periods in the mid-1970s and 1980s when heavy ice conditions were not favourable for ringed seals to maintain breathing holes and birth lairs, the productivity and survival of both ringed seals and polar bears declined (Stirling 2002). Given that polar bears may feed primarily on newly weaned ringed seal pups (Stirling and Oritsland 1995), the proportion of ringed seal in polar bear diets may reflect favourable environmental conditions for both species (Pilfold et al. 2015; Hamilton et al. 2017).

Although ringed seals are the primary prey of polar bears across the circumpolar Arctic, bears also feed on locally available prey, including bearded seals (*Erignathus barbatus*; Thiemann et al. 2007, 2008a), harp seals (*Pagophilus groenlandica;* Derocher et al. 2002; Galicia et al. 2015), harbour seals (*Phoca vitulina;* Thiemann et al. 2008a; Sciullo et al. in press), walruses (*Odobenus rosmarus;* Calvert and Stirling 1989), beluga whales (*Delphinapterus leucas;* Freeman 1973), narwhals (*Monodon monoceros;* Smith and Sjare 1990), and the carcasses of bowhead whales (*Balaena mysticetus;* Bentzen et al. 2007; Schliebe et al. 2008; Herreman and Peacock 2013; Galicia et al. 2016). The relative importance of alternative prey

(i.e., other than ringed seal) may vary both spatially and temporally according to sea-ice conditions (Hamilton et al. 2017), prey life history (Young et al. 2015), and seasonal habitat use (Hornby et al. 2017). Polar bear diet may also vary within a subpopulation due to differences in body size and energetic requirements. Adult male polar bears are approximately twice the size of adult females (Derocher et al. 2005), allowing them to potentially hunt large-bodied prey species (i.e., bearded seals) more easily (Thiemann et al. 2007, 2008a; Derocher et al. 2010).

Polar bears have highly seasonal feeding habits, becoming hyperphagic when prey is abundant, and relying on stored energy (i.e., fasting) when prey is limited (Stirling and McEwan 1975; Stirling and Oritsland 1995). As stored energy is mobilized from adipose tissue, the proportion of lipid (relative to non-lipid components) will decline (Pond 1992). Thus, the relative lipid content of adipose tissue can serve as an indicator of body condition in polar bears (i.e., Thiemann et al. 2006; Sciullo et al. 2016).

Adipose tissue lipids are primarily composted of fatty acids (FA), and the relative abundance of multiple FA (i.e., the FA profile or "signature") can reflect recent diet, as ingested FA are predictably incorporated into a consumer's fat stores (Ackman and Eaton 1966; Iverson et al. 2004; Budge et al. 2006; Thiemann et al. 2008a, 2008b). Quantitative fatty acid signature analysis (QFASA; Iverson et al. 2004) is a multivariate least squares model that uses the FA signatures of a predator and its potential prey to generate quantitative estimates of predator diet. The model determines the proportional combination of prey signatures that comes closest to matching the observed predator after accounting for FA-specific patterns of metabolism (Iverson et al. 2004).

The Southern Beaufort Sea (SB) subpopulation of polar bears has experienced recent demographic decline, with estimated abundance falling 25-50% from 2004 to 2006 followed by a

period of stability through 2010 (Bromaghin et al. 2015). In contrast, the adjacent Northern Beaufort Sea (NB) subpopulation remained largely stable through the mid-2000s (Stirling et al. 2011). The ecological drivers of these divergent temporal trends are not well understood, although the demographic decline in SB was correlated with a period of sea ice decline that may have negatively affected the ability of polar bears to access their prey (Bromaghin et al. 2015).

I used lipid analyses and QFASA to quantify the diet composition and body condition of polar bears harvested in the Canadian Beaufort Sea from 1999-2015, a period of substantial habitat change. The objective of this study was to examine environmental drivers of variation in diet composition, in addition to spatial, temporal, seasonal, and age- and sex-specific variation, and the implications on body condition. I hypothesized that polar bear diet composition and body condition would be affected by variation in regional sea ice conditions, resulting in differences in diet and foraging success (i.e., body condition) over time. I further hypothesized that differences in diet and body condition across bears of different age classes and sexes would result from the ability of adult males to capture larger-bodied prey. A better understanding of the relationship between apex predators, prey, and environmental condition is necessary for proactive management and conservation of Arctic marine mammals.

Methods

Sample Collection

I used adipose tissue samples collected from 521 polar bears harvested by local Inuvialuit subsistence hunters in the Inuvialuit Settlement Region of the western Canadian Arctic from 1999 to 2015. Bears belonged to two subpopulations: NB and SB (Figure 2.1; International Union for the Conservation of Nature, Polar Bear Specialist Group;

http://pbsg.npolar.no/en/status/population-map.html). Seasons were based on the date the polar bear was harvested, where I defined winter/spring as January – June and summer/fall as July – December; sampling in the winter/spring was primarily from February – May, and sampling in summer/fall was primarily in November (Fig. 2S.1). It is illegal to harvest family groups (i.e., adult females with dependent cubs) so sampled bears included males and females of all independent age classes (Table 2.1; defined as: adults = 5+ years old; subadults = 3-4 years old; and 2-year olds). Age was determined by counting growth layer groups in the cementum of an extracted vestigial premolar tooth (Calvert and Ramsay 1998). Samples of subcutaneous adipose tissue (approx. 8 cm x 4 cm) were collected from the rump of each bear and individually wrapped in aluminum foil, sealed in a Whirl-Pak, and stored at – 20°C until analysis.

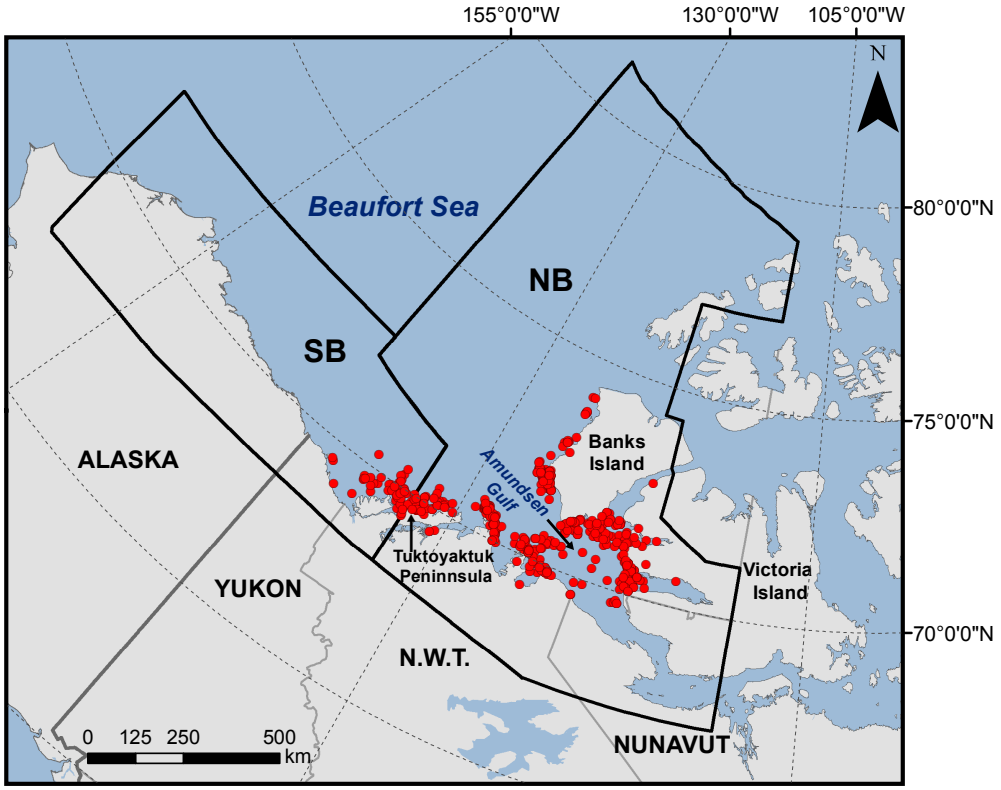

Figure 2. 1 Locations of polar bears (red circle) harvested in the Inuvialuit Settlement Region from 1999-2015. Bears were located in the subpopulation boundaries of the Southern Beaufort Sea (SB) or the Northern Beaufort Sea (NB).

Table 2. 1 Number of polar bear samples used in the lipid and fatty acid analyses from 1999-2015 in the Canadian Beaufort Sea.

Year	Total no. samples	Subpopulation total		2-year-old		Subadult			Adult			?	
		NB	SB	F	M	F	M	?	F	M	?	F	M
1999	7	3	4				2			5			
2000	1	1							1				
2001	7	7			1		1		2	3			
2003	49	45	4	5	3	9	13		4	15			
2004	49	38	11	3	1	10	13		5	17			
2005	39	33	6		3	6	5		4	21			
2006	29	28	1		1	6	2		6	12		1	1
2007	38	35	3		1	3	8		7	17		2	
2008	25	22	3	1		2	4	1	8	8			1
2009	23	22	1	1		1	2	1	1	12	1	2	2
2010	16	15	1	3		1	1		3	7		1	
2011	62	53	9	1	6	7	13		15	18		2	
2012	67	57	10	2	6	11	17		10	19		1	1
2013	44	39	5		3	7	15		4	12			3
2014	34	33	1	2	6	4	7		3	9		1	2
2015	18	18								2		6	10
?	13	10	3										
Total	**521**	**459**	**62**	**18**	**31**	**67**	**103**	**2**	**73**	**177**	**1**	**16**	**20**

? = unknown

Other recent work has used QFASA to examine the diets of polar bears in the adjacent Chukchi Sea subpopulation, so to make our results comparable, I used the prey FA library from Bromaghin et al. (2015; https://alaska.usgs.gov/products/data.php?dataid=44), which included ringed seals (n = 222), bearded seals (n = 82), beluga whales (n = 29), and bowhead whales (n = 64). I also included blubber samples from 50 ringed seals harvested in 2015 by Inuvialuit hunters in the eastern Amundsen Gulf, for a total prey library of 447 individual animals. As with polar bear adipose tissue, marine mammal blubber was sampled from skin to muscle, wrapped in aluminum foil, sealed in a Whirl-Pak, and stored at – 20°C until analysis.

Laboratory Analyses

I subsampled the interior of polar bear adipose tissue and marine mammal blubber samples (approx. 0.3 g) to avoid any oxidized tissue (Budge et al. 2006). Tissue subsamples were then

weighed and lipid was quantitatively extracted using a Folch extraction (Folch et al. 1957), as modified by Iverson et al. (2001). Lipid content was expressed as the percent of total sample wet weight ± 1 standard error as an index of body condition (Thiemann et al. 2006; McKinney et al. 2014; Sciullo et al. 2016). FA methyl esters (FAME) were derived from the extracted lipid using sulfuric acid in methanol as a catalyst (Thiemann et al. 2004; Budge et al. 2006). FAME were analyzed in duplicate on a temperature-programmed gas chromatograph (GC) with a flame ionization detector fitted with a polar column (30 m x 0.25 mm inner diameter; DB-23; Agilent Technologies, Palo Alto, California, USA; Budge et al. 2006). FA were measured as a mass percent of total FA ± 1 standard error, and expressed by the shorthand nomenclature of *A*:*B*n-*X*, where *A* is the length of the carbon chain, *B* is the number of double bonds, and *X* is the position of the first double bond relative to the terminal methyl group. FA identifications were based on retention times and were manually verified and corrected using CompassCDS software (Version 3.0, Bruker Daltonics Inc., Germany).

QFASA Modelling

The QFASA method developed by Iverson et al. (2004) generates estimates of predator diets by modelling the predator signature as a linear combination of available prey signatures and determining the combination of prey that minimizes the distance between the observed and modelled predator. Calibration coefficients, as derived from captive mink (*Neovison vison*), were used to account for FA-specific patterns of modification and biosynthesis that occur from ingestion to deposition in the consumer's adipose tissue (Iverson et al. 2004; Thiemann et al. 2008b). I generated estimates of diet composition, using the Aitchison distance measure, for each individual polar bear using the est_diet() function in the R package *qfasar* (Bromaghin 2017). I also used a new diagnostic function to generate a jackknifed cross-validation of the prey library,

the leave-one-prey-out analysis (function: lopo()), which temporarily removes each individual prey sample from the prey library and models it as a diet estimate, as if it were a predator, before returning it to the prey library. This is done for each prey sample, and means are calculated for each species, which yields a measure of the prey types' distinctiveness within the library. To determine the suite of FA to use in QFASA modelling, I started with the dietary set used by Galicia et al. (2015) and removed each FA in turn, ran the leave-one-prey-out (LOPO) analysis, and investigated the accuracy of prey classifications. LOPO outputs the mean distribution of estimates among all prey types; perfect estimation yields values of 1 for each prey type (Bromaghin 2017). If LOPO analysis showed more accurate (i.e., higher) values upon FA removal, I removed the respective FA from QFASA diet estimations. QFASA diet estimation and diagnostics were conducted using R (version 3.4.0, GUI 1.40, R Development Team 2017).

Sea-Ice Data

I used sea-ice data from the National Snow and Ice Data Center (NSIDC; Boulder, CO), as summarized by Stern and Laidre (2016). Briefly, daily sea ice data were measured by satellites Nimbus-7 SSM and DMSP SSM/I-SSMIS Passive Microwave Data at a cell size of 25 x 25 km daily. Stern and Laidre (2016) derived yearly values for four sea-ice metrics in SB and NB: date of sea-ice break-up, date of sea-ice freeze-up, duration of open water season, and mean summer sea-ice concentration. A threshold for each year was calculated as the mid-way point between the March mean sea ice concentration and the September mean sea ice concentration. Date of sea ice freeze-up and date of sea ice break-up were calculated as the day of year that sea ice concentration crossed above or below the year's threshold, respectively. Duration of the open water season was calculated as the number of days' difference between sea ice break-up and

freeze-up. Mean summer sea-ice concentration was calculated for 1 June – 31 October for each year.

Statistical Analyses

I used principal component analysis (PCA) to reduce the number of FA variables to examine potential structure in both the polar bear and prey FA data (bolded in Tables 2S.1 - 2S.3). Prior to conducting PCA, I transformed all FA data to the log ratio of each FA to 18:0 (Budge et al. 2006) using the equation $x_t = \log(y_i/x_i)$, where x_i is the geometric mean of the FA data for the sample, y_i is the original FA data expressed as a proportion of the total signature amounting to 1.0, and x_t is the transformed FA data (Budge et al. 2006). The number of principal components (PC) that were used in further analyses was determined using the broken-stick model (Jackson 1993), where PC axes were retained when their eigenvalues (a measure of component variance) were larger than the value given by the broken-stick model. PC axis scores for polar bear FA were used in one-way MANOVA with subpopulation, sex, age class, and season as factors, separately. I also examined interactions between all factors and PC scores for spatial, seasonal, and demographic effects.

I used similar PCA methods to analyze the FA of prey species to examine potential clustering within the prey library, to ensure the model would be able to accurately distinguish between prey species. I would expect any clustering to be due to ecological (i.e., similarity in foraging) and phylogenetic patterns (Budge et al. 2006; Thiemann et al. 2008b).

I used a redundancy analysis (RDA; van den Wollenberg 1977) and a forward-selection model to examine the minimum number of variables that significantly influence polar bear diet, and ranked the models (i.e., each successive step in the forward selection model as it is building) using Akaike information criterion (AIC) to identify variables that explained the most variation

in the response variables (Borcard et al. 1992). The RDA included all intraspecific (i.e., age, age class, sex), spatial (i.e., longitude, latitude, subpopulation), temporal (i.e., ordinal date, month, season, year), and environmental (i.e., sea-ice break-up, freeze-up, duration of open-water season, mean summer sea-ice concentration) predictor variables. Prior to RDA modelling I transformed the diet data (response variables) using the Hellinger transformation, which takes the square root of the sum of each proportion per prey species, reducing skewedness of more prominent response variables (i.e., ringed seal proportion; Legendre and Gallagher 2001).

Results from the RDA indicated which variables were driving polar bear diet; I further analyzed differences between significant binary variables (i.e., sex, subpopulation, season) using permutation MANOVA, as diet estimates were proportional and therefore not normally distributed. I tested for age-, longitudinal-, and year-effects using Spearman's rank correlations for each species' contribution to polar bear diet, when separated by sex. Year was used for NB bears, but due to low sample sizes in SB (Table 2.1) bears were binned for three time periods: 1) 2003-2006, a period of low survival and population decline, 2) 2007-2010, where adult survival improved and the population stabilized (Bromaghin et al. 2015), and 3) 2011-2014, a period of unknown survival. Where relevant, I also tested for subpopulation, sex, age class, and seasonal differences in each prey types' contribution to polar bear diet using a permutation one-way ANOVA. I used Spearman's rank correlations to examine the relationship between polar bear diet and body condition (i.e., percent lipid in the adipose tissue) independently for each prey type.

Temporal trends in sea ice metrics were tested using linear regressions. The relationship between each sea-ice metric and the proportion of each prey in polar bear diets was also tested in a linear regression, of NB adult and subadults, separated by sex; SB bears were not included due

to small sample size in some years (Table 2.1). Similarly, I used linear regressions to investigate the relationship between sea ice conditions and body condition of bears in NB, separated by sex. Since bears harvested in the winter/spring season (Jan – April) were mostly killed in February-March, their foraging ecology would not be influenced by the date of sea ice break-up, freeze-up, duration of the open water season, or summer sea ice concentration of that year; thus, winter/spring bears were compared against the sea ice break-up, freeze-up, duration of open water season, and summer sea ice concentration in the year prior to sampling. All statistical analyses were conducted using R (version 3.4.0, GUI 1.40, R Development Team 2017).

Results

Fatty Acid Profiles

PCA of polar bear FA profiles explained 71.2% of variance in the first two PC axes (Table S5). A MANOVA conducted on PC1-PC2 scores revealed differences in dietary FA between polar bears harvested in the NB and the SB subpopulations (Wilks' $\lambda = 0.98$, $F_{(2,468)} = 4.179$, $p = 0.016$). FA signatures also differed across sex (Wilks' $\lambda = 0.93$, $F_{(4,934)} = 8.601$, $p < 0.001$), age class (MANOVA, Wilks' $\lambda = 0.98$, $F_{(4,934)} = 2.869$, $p = 0.022$), and season (Wilks' $\lambda = 0.92$, $F_{(2,464)} = 20.016$, $p < 0.001$). Furthermore, dietary FA signatures were different between bears of different age classes after accounting for subpopulation (Wilks' $\lambda = 0.97$, $F_{(4,880)} = 3.59$, $p = 0.006$), but not for different age classes after accounting for subpopulation and sex (Wilks' $\lambda = 0.98$, $F_{(4,880)} = 2.143$, $p = 0.074$), nor males and females in different age classes (Wilks' $\lambda = 0.96$, $F_{(6,880)} = 0.415$, $p = 0.941$), or between bears harvested in different subpopulations after accounting for sex (Wilks' $\lambda = 0.99$, $F_{(2,440)} = 0.415$, $p = 0.660$).

A PCA of the prey FA profiles explained 67.22% of the variance in the first 4 PC axes. A permutation MANOVA on the first 4 PC axes confirmed species-species differences among

the four prey species (Fig. 2.2; F = 26597, R^2 = 0.995, p = 0.039). Bearded seal FA signatures were dominated by 16:1n-7, 18:1n-9, and 18:1n-7; whereas ringed seal was also dominated by 16:1n-7, 18:1n-9, and 22:6n-3. Beluga whale blubber was also dominated by 16:1n-7 and 18:1n-9, but also 20:1n-9; similarly, bowhead whale FA profiles were characterized by high levels of 16:1n-7, 18:1n-9, with the third largest contribution being from FA 16:0. Leave-one-prey-out analysis revealed the clearest separation between prey FA signatures when FA 20:1n-11 and 22:1n-9 were omitted. Leave-one-prey-out allocation accuracy for the final set of 29 FA was 0.92 for bearded seal and beluga whale, 0.97 for bowhead whale, and 0.86 for ringed seal, thus, 20:1n-11 and 22:1n-9 were excluded from QFASA diet estimations. Among ringed seal, misallocated samples were most commonly attributed to bearded seal and beluga whale.

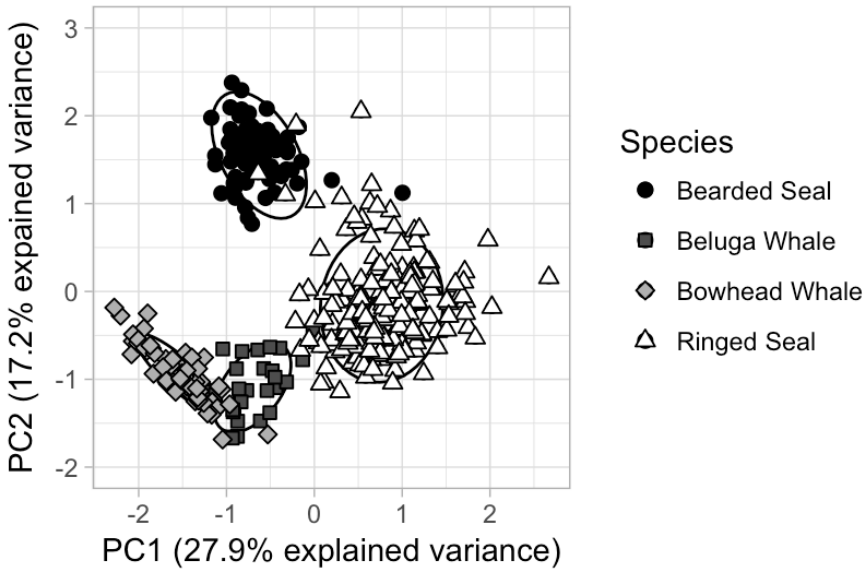

Figure 2. 2 Principal component analysis of prey library dietary fatty acids.

General Dietary Patterns

The mean diet composition of all polar bears harvested in the Beaufort Sea across all years and seasons in the study was 14.6% bearded seal, 17.6% beluga whale, 10.2% bowhead whale, and

57.7% ringed seal (Fig. 2.3). Polar bear diets were dominated by ringed seals irrespective of bear sex, season, or age class.

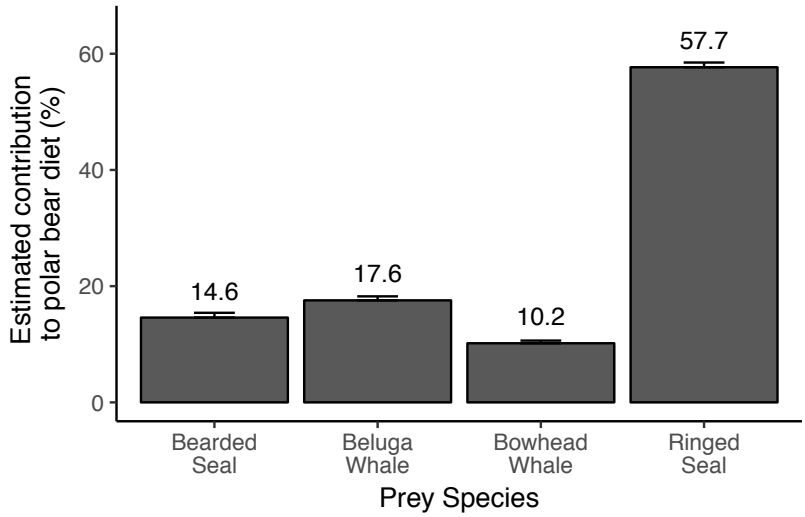

Figure 2. 3 Mean (±SE) dietary composition of polar bears harvested in the Canadian Beaufort Sea from 1999 to 2015. This includes bears of all age classes and both sexes.

Longitude, as the only variable, was the best-fitting model of potential factors influencing polar bear diet (Table 2.2; as determined by AIC; $p = 0.002$). Models including sex, and combining sex and age were considered the second and third best fitting models; additionally, age class, date of sea ice freeze-up and break-up, year, season, and ordinal date were also significant covariates (Table 2.2).

Table 2. 2 Redundancy analysis (RDA) candidate models evaluating the best-fitting model of factors influencing the diet of polar bears in the Canadian Beaufort Sea from 1999 to 2015. Akaike Information Criterion (AIC) was used as the main criteria for model selection. Variables: longitude = long; age class = ac; date of sea ice freeze-up = sif; date of sea ice break-up = sib; ordinal date = od.

Model	RDA forward-selection model		
	AIC	F	p-value
long	-812.03	21.108	0.002
long + sex	-828.98	19.259	0.002
long + sex + age	-841.71	14.849	0.002
long + sex + age + ac	-846.40	6.668	0.004
long + sex + age + ac + sif	-851.54	7.098	0.002
long + sex + age + ac + sif + sib	-856.63	7.029	0.004
long + sex + age + ac + sif + sib + year	-859.39	4.694	0.004
long + sex + age + ac + sif + sib + year + season	-861.01	3.549	0.02
long + sex + age + ac + sif + sib + year + season + od	-867.31	8.186	0.002

Spatial Patterns

Longitude of sampling location explained the most variation in diet composition (Table 2.2). Male, but not female, adult and subadult bears had significant longitudinal trends of proportional consumption of each prey type (Fig. 2.4). Male proportional consumption of bearded seal (rho = -0.352, S = 3738400, $p < 0.001$) and bowhead whale (rho = -0.150, S = 3177400, $p = 0.017$) decreased, and beluga whale (rho = 0.349, S = 1800200, $p < 0.001$) and ringed seal (rho = -0.137, S = 2384300, $p = 0.028$) increased, as sample location moved from west (i.e., Tuktoyaktuk Peninsula, western Banks Island) to east (i.e., Amundsen Gulf; Fig. 2.1; Fig. 2.4-2.5). Most generally, diet composition of polar bears in NB was different than bears in SB (Fig. 2.6; $R^2 = 0.008$, $p = 0.016$).

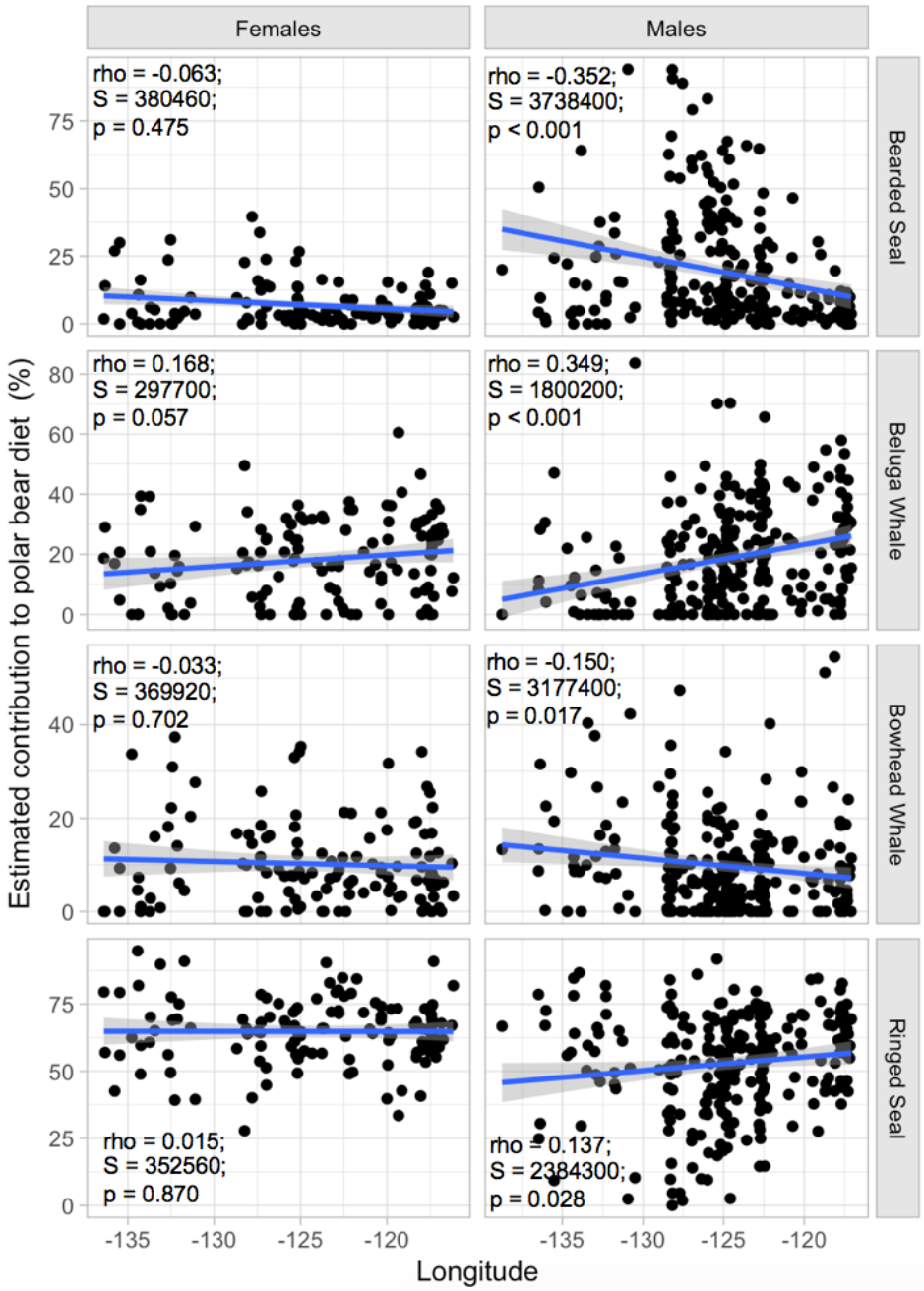

Figure 2. 4 Effect of longitude on estimated contribution of prey species to the diet of adult and subadult bears sampled in the western Canadian Arctic from 1999-2015. Statistical results from Spearman rank correlation are shown on the figure, with a linear trendline and 95% confidence intervals indicated by grey shading.

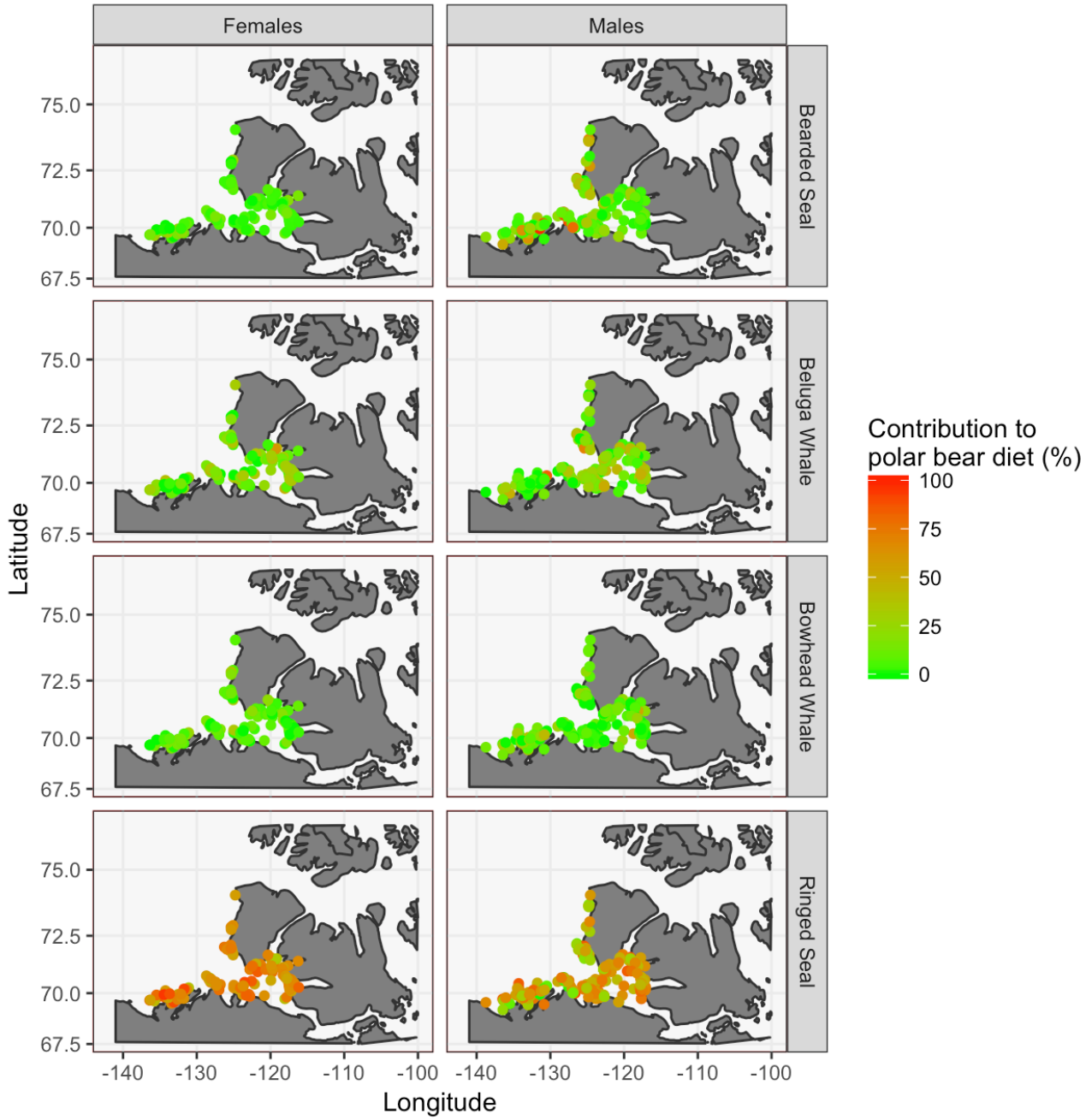

Figure 2. 5 Spatial trends in adult and subadult polar bear diet composition from 1999 to 2015.

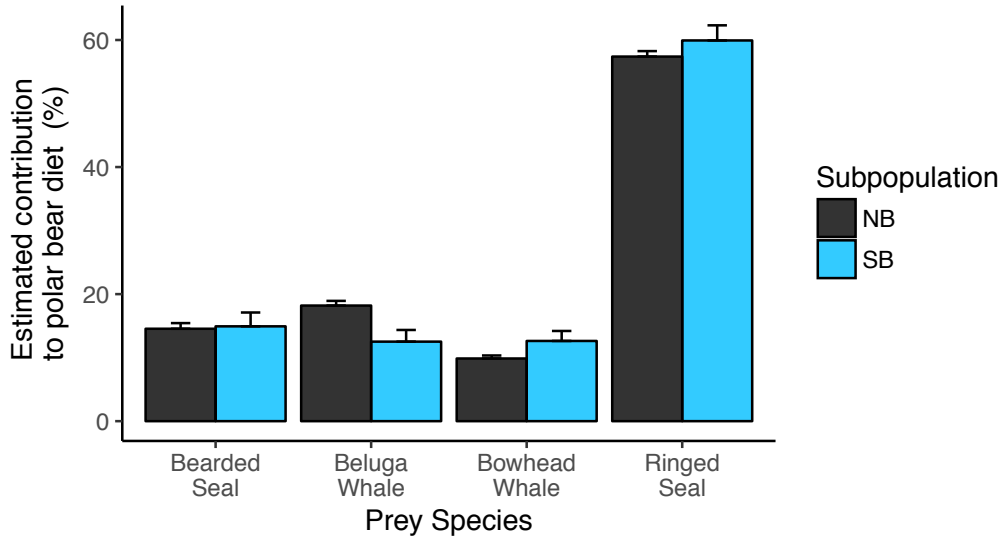

Figure 2. 6 Diet composition (mean ± SE) of polar bears sampled in the Northern Beaufort Sea (NB) and Southern Beaufort Sea (SB) subpopulations from 1999-2015.

Intraspecific Patterns

Polar bear diet composition differed between males and females ($p = 0.001$); males consumed proportionately more bearded seal ($p < 0.001$) and less ringed seal than females ($p < 0.001$), but there was no difference between male and female consumption of beluga whale or bowhead whale ($p = 0.961$, $p = 0.235$, respectively). Polar bears also differed across age classes ($p = 0.001$) in their consumption of bearded seals ($p < 0.001$, adults highest), beluga whale ($p = 0.012$, adults highest), and ringed seal ($p < 0.001$, 2-year-olds and subadults highest), but not bowhead whale ($p = 0.216$). Specifically, males in the NB increased proportional consumption of bearded seal (Fig. 2.7; rho = 0.431, S = 1573400, $p < 0.001$), and decreased consumption of ringed seal with age (rho = -0.401, S = 3871600, $p < 0.001$). There were no significant trends between age and proportional consumption of any prey type for male or female bears in SB (Fig. 2.8), or for females in NB (Fig. 2.7). There were no significant interactions between sex and

subpopulation ($p = 0.314$), sex and age class, ($p = 0.108$), or sex, subpopulation, and age class ($p = 0.396$) in polar bear diet composition.

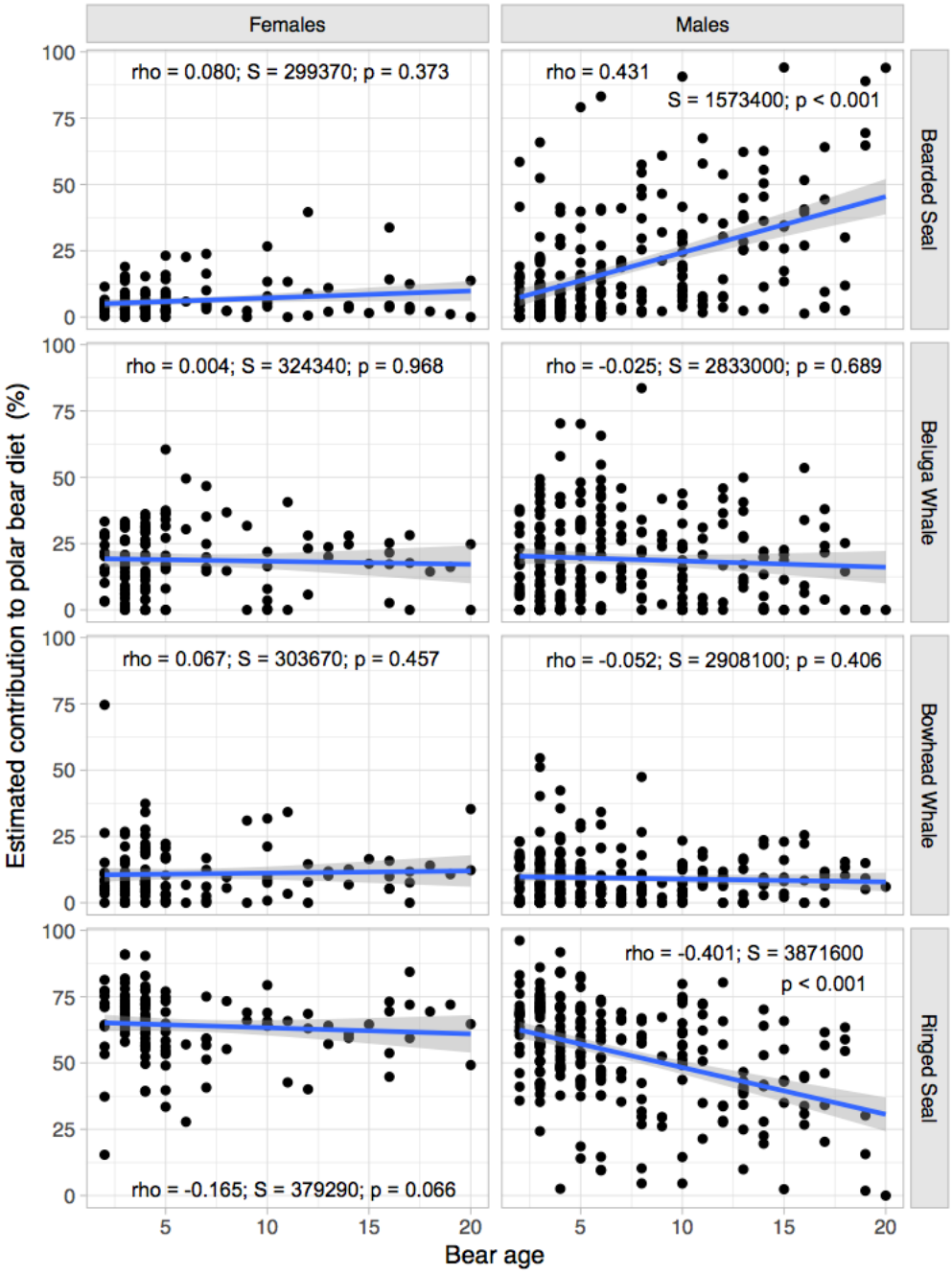

Figure 2. 7 Effect of polar bear age on estimated contribution of prey species to the diet of bears harvested in the Northern Beaufort Sea subpopulation from 1999-2015. Statistical results from Spearman rank correlation are shown on the figure, with a linear trendline and 95% confidence intervals indicated by grey shading.

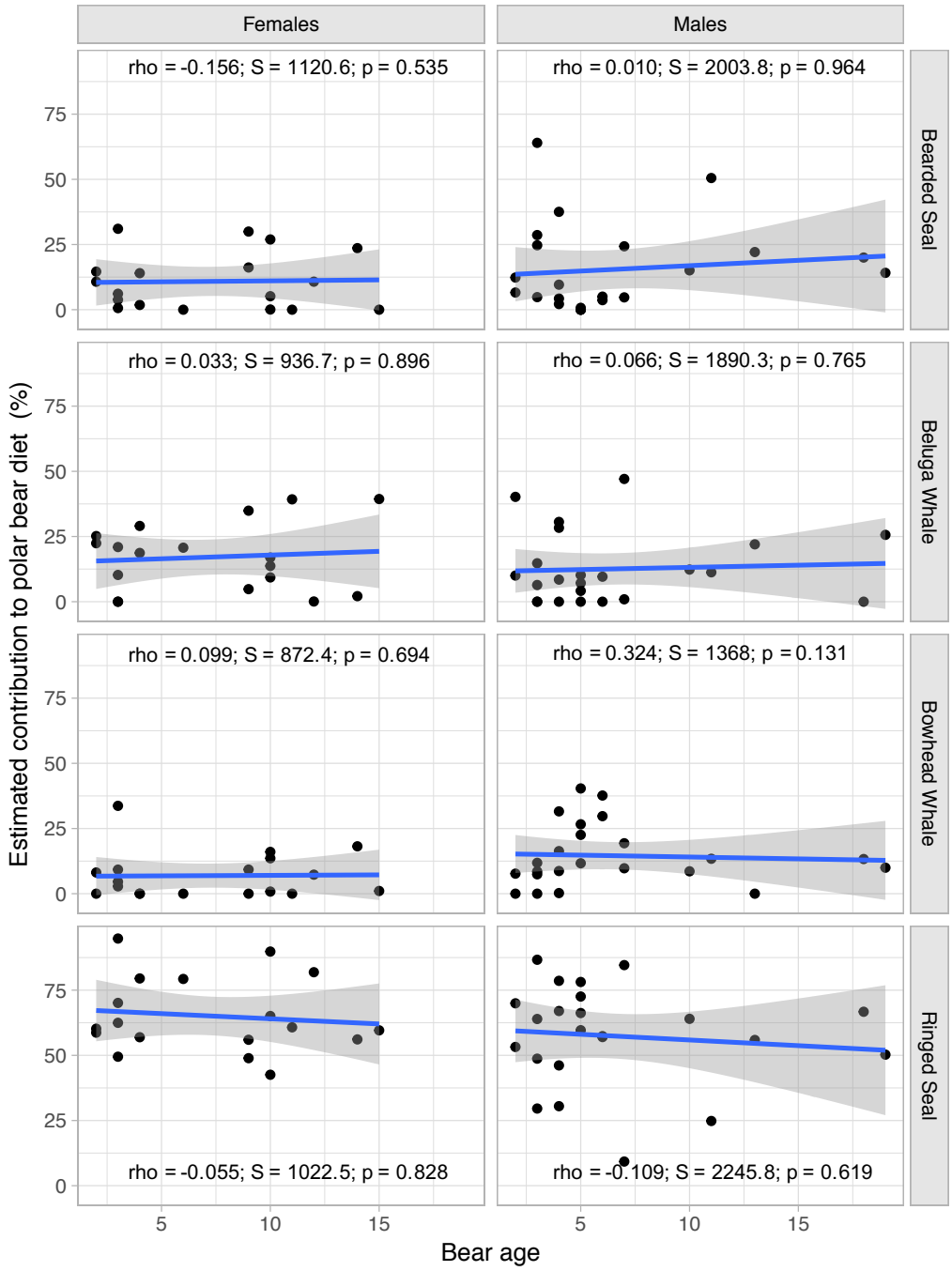

Figure 2. 8 Effect of polar bear age on estimated contribution of prey species to the diet of bears harvested in the Southern Beaufort Sea subpopulation from 1999-2015. Statistical results from Spearman rank correlation are shown on the figure, with a linear trendline and 95% confidence intervals indicated by grey shading.

Seasonal Trends

When polar bears from NB and SB were pooled, diets differed between the summer/fall and winter/spring (Fig. 2.9; $p = 0.007$). In females, bearded seal consumption was significantly higher in the summer/fall than the winter/spring ($p = 0.001$), whereas beluga whale, bowhead whale, and ringed seal consumption was not significantly different between seasons ($p = 0.167$, $p = 0.298$, $p = 0.902$ respectively). Male polar bears consumed the same amount of bearded seal, bowhead whale, and ringed seal in the summer/fall and winter/spring ($p = 0.745$, $p = 0.321$, $p = 0.863$, respectively). Beluga whale contributed more to the diet of male polar bears harvested in the winter/spring than the summer/fall ($p = 0.003$).

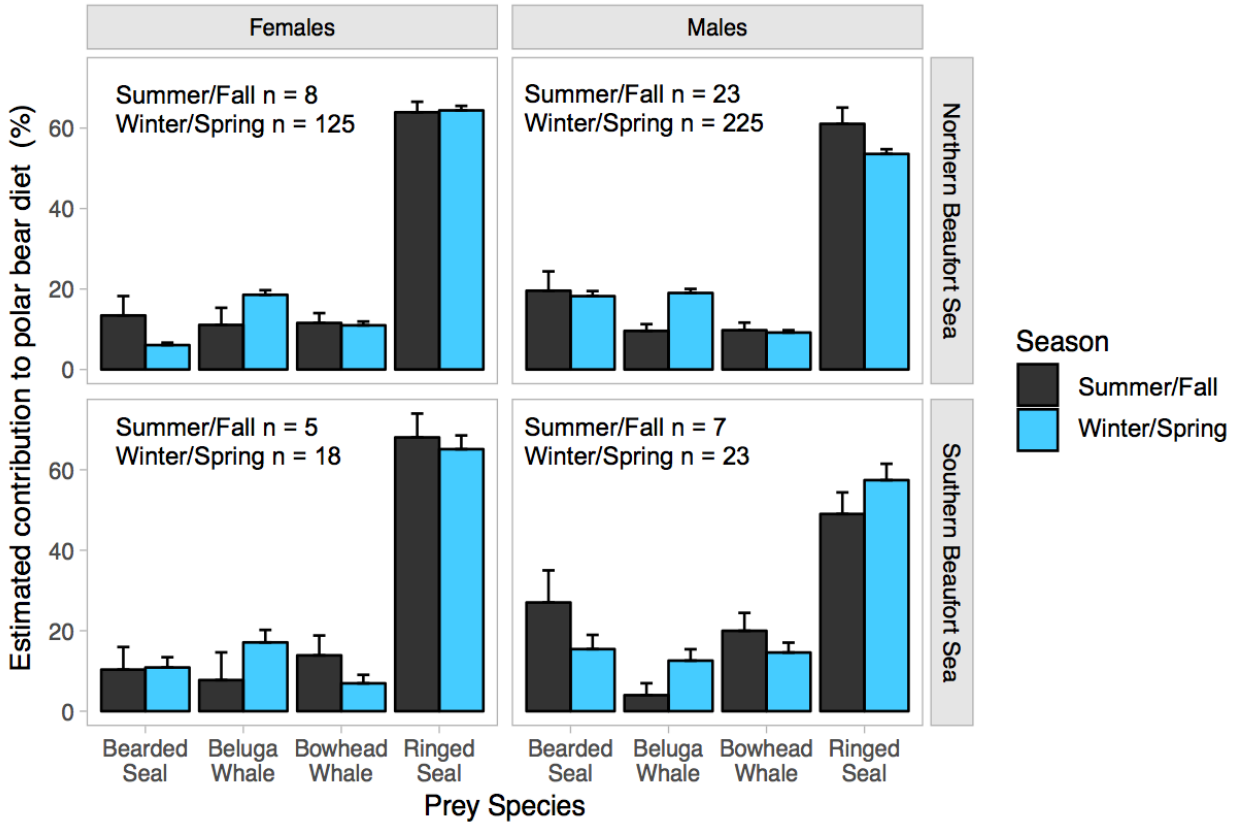

Figure 2. 9 Polar bear diet composition (mean ± SE) of bears harvested in the summer/fall and winter/spring in the Canadian Beaufort Sea from 1999-2015 (unknown sex or season: n = 7).

Body Condition and Diet

Body condition was significantly higher in bears harvested in NB than in the SB subpopulation (Fig. 2.10; permutation ANOVA, $p = 0.020$), but was not different between sexes ($p = 0.263$) or age classes ($p = 0.121$). Body condition was not affected by the proportional consumption of any prey type of male or female polar bears sampled in NB, however there was a positive correlation between ringed seal consumption and body condition (Fig. 2.11; rho = 0.545, S = 920, $p = 0.008$) in SB females, and a negative correlation between beluga whale consumption and body condition (rho = -0.580, S = 6415.4, $p = 0.001$) in SB male polar bears.

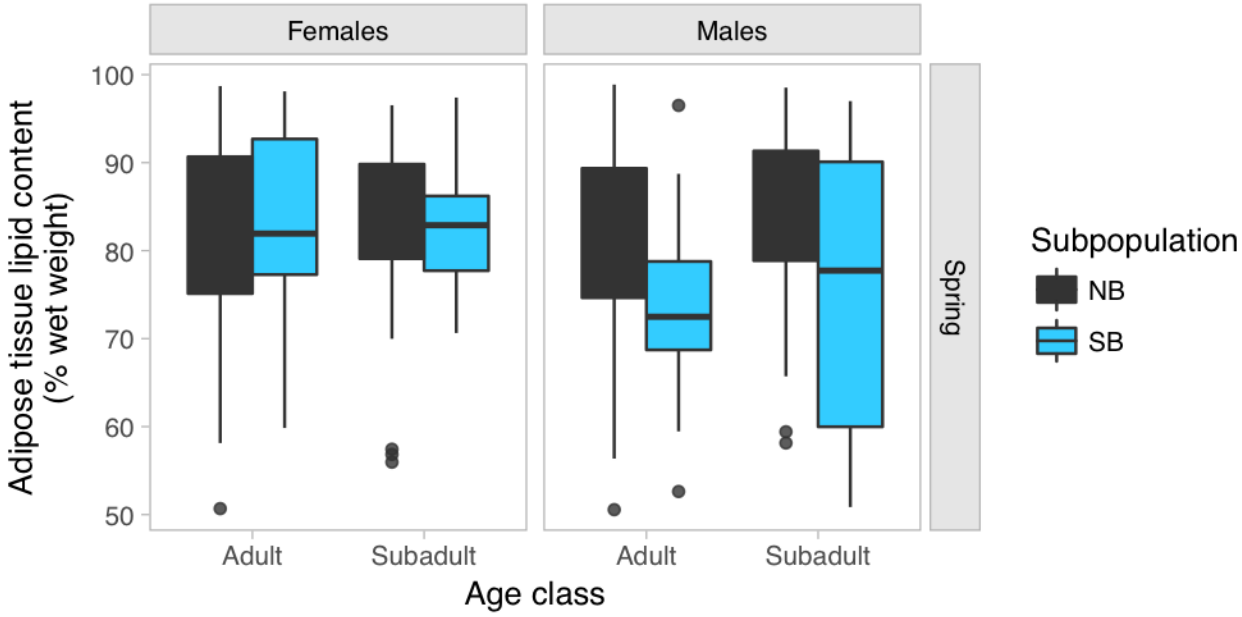

Figure 2. 10 Body condition (adipose tissue lipid content) of polar bears sampled in the Winter/Spring in the Northern Beaufort Sea (NB) and Southern Beaufort Sea (SB) subpopulations form 1999-2015.

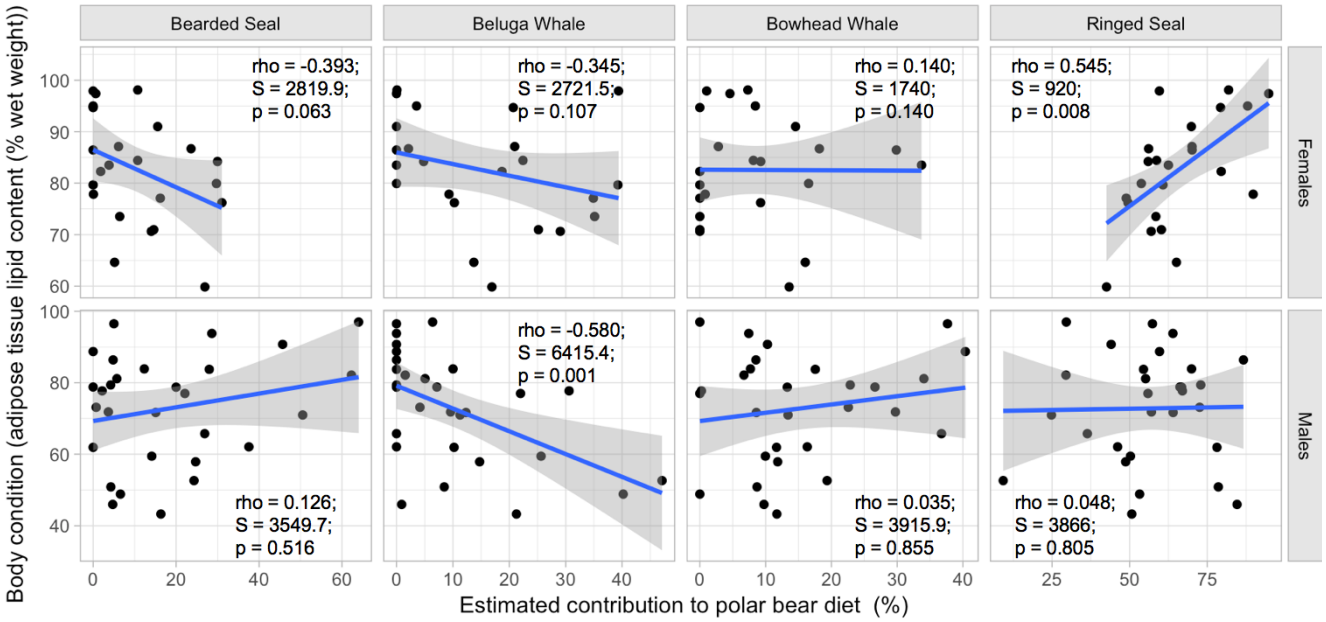

Figure 2. 11 Effect of body condition (adipose tissue lipid content) on diet composition of polar bears (of all ages) sampled in the Southern Beaufort Sea (SB) from 1999-2015. Statistical results from Spearman rank correlation are shown on the figure, with a linear trendline and 95% confidence intervals indicated by grey shading.

Temporal Trends

Ringed seal remained the primary prey of polar bears in all years, for both males and females, with interannual variation (Fig. 2.12). Beluga whale consumption was higher in congruent years when ringed seal consumption was reduced in NB. Both male and female adults and subadults in NB showed a decrease in ringed seal in 2007, and only females showed a decline in ringed seal in 2010. Overall, diet did not change linearly for any prey type in NB. Diet composition and body condition varied in SB, with lower values of ringed seal consumption and body condition in 2011-2014 than earlier years (i.e., 2003-2006 and 2007-2010; Fig. 2.13). Bowhead whale consumption was highest, and beluga whale and bearded seal consumption was lowest in 2007-2010 relative to 2003-2006 and 2011-2014 (Fig. 2.13).

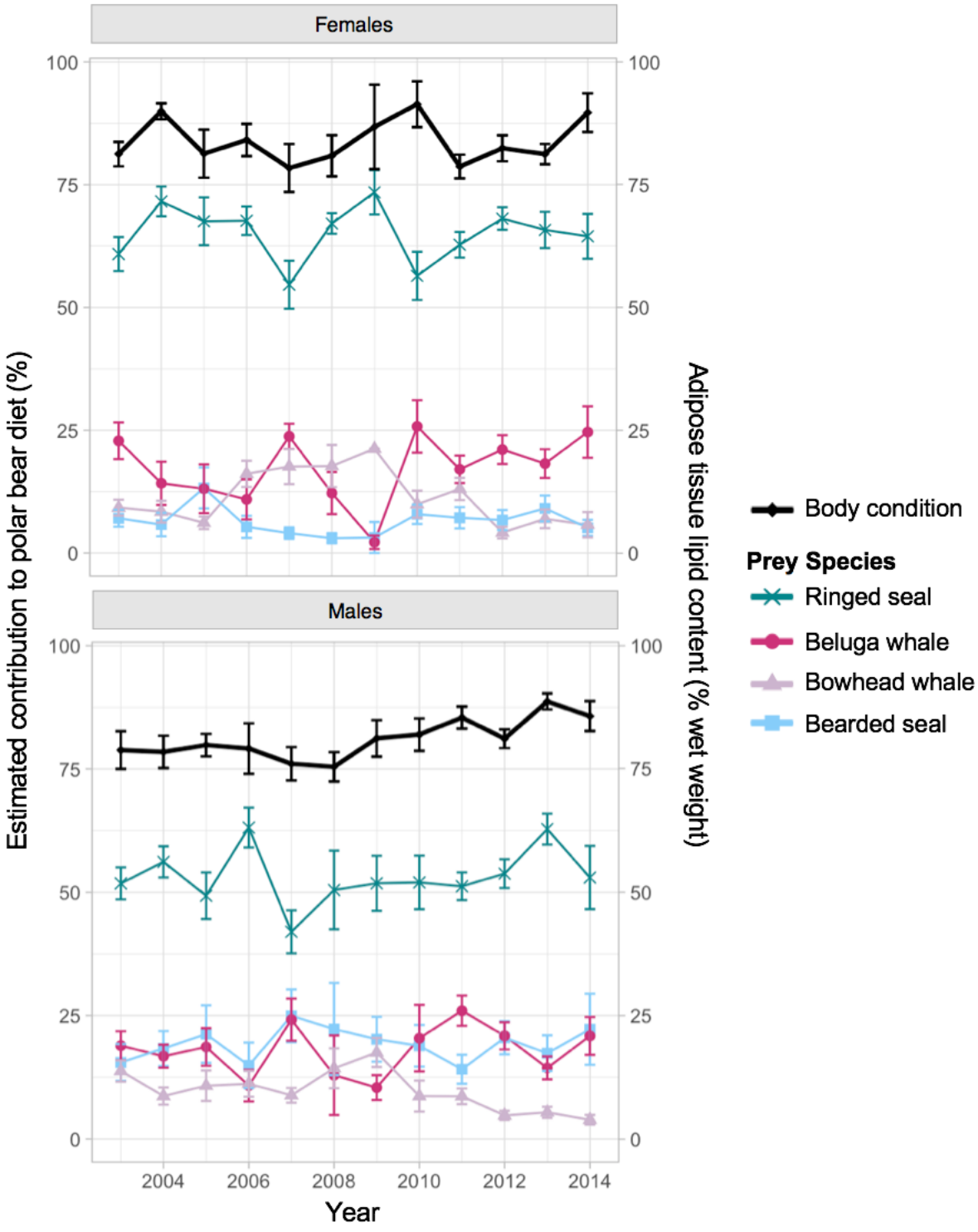

Figure 2. 12 Temporal trend in polar bear diet composition and body condition (expressed as adipose tissue lipid content; mean ± SE) for adult and subadult bears in the Northern Beaufort Sea subpopulation.

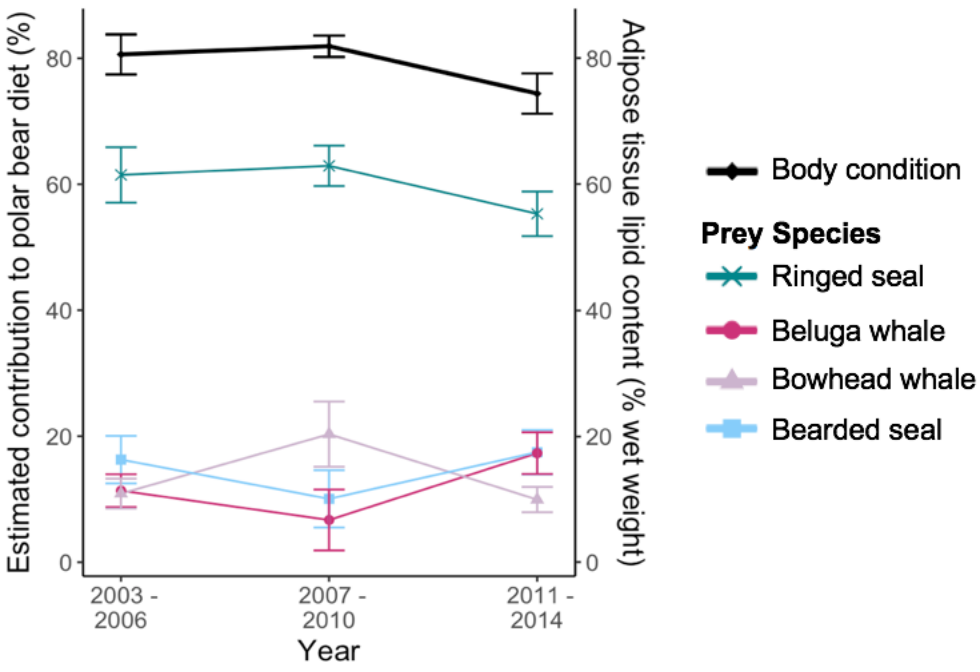

Figure 2. 13 Temporal trend in polar bear diet composition and body condition (expressed as adipose tissue lipid content; mean ± SE) for bears of all age classes and both sexes in the Southern Beaufort Sea subpopulation. Bears were binned from 2003-2006 (n = 22), 2007-2010 (n = 8), and 2011-2014 (n = 25).

Sea-Ice

Sea-ice freeze-up in both NB and SB occurred progressively later in the year and the duration of open water season increased over the course of my study (1999-2015). Moreover, sea-ice break-up occurred progressively later and summer sea-ice concentration declined over the study period in SB but not NB (Fig. 2.14).

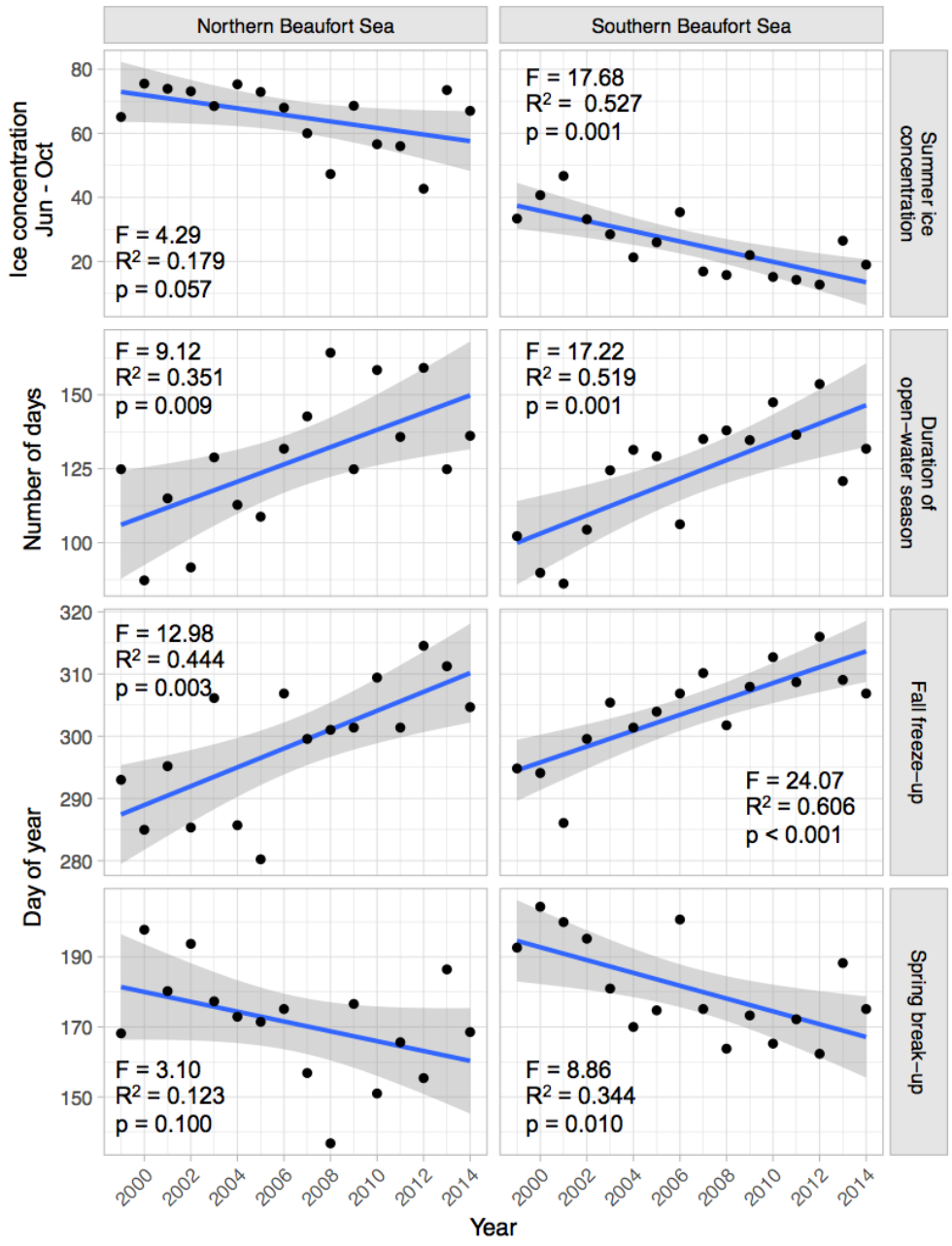

Figure 2. 14 Temporal trends in sea-ice metrics in the Northern and Southern Beaufort Sea polar bear subpopulations. Data from Stern and Laidre (2016). Statistical results from linear regression are shown on the figure, with linear trendline and 95% confidence intervals indicated by grey shading.

Sea-ice freeze-up and summer sea-ice concentration had no significant effect on polar bear diet in NB (Table 2.5; Fig. 2.15). For NB adult and subadult females, sea-ice break-up was positively

related to the proportion of beluga whale ($F = 7.600$, $R^2 = 0.398$, $p = 0.022$), but not related to the proportion of other prey types in the diet, however, there was a non-significant negative trend between the date of spring break-up and consumption of bowhead whale and ringed seal (Fig. 2.15). The diets of NB adult and subadult males were not significantly affected by any of the sea-ice metrics (Table 2.5).

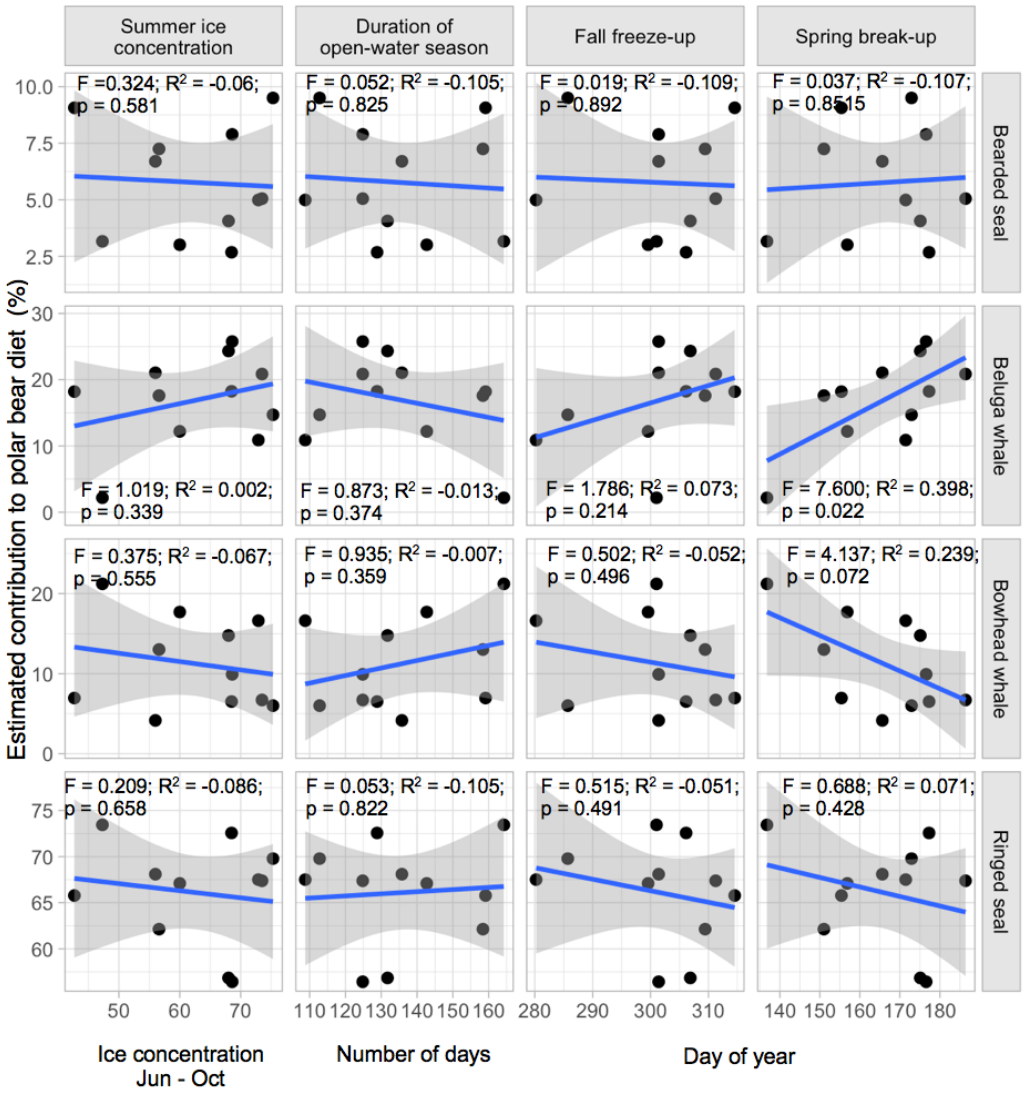

Figure 2. 15 Effects of sea ice conditions (data from Stern and Laidre (2016)) on (year-mean) diet composition of adult and subadult female polar bears sampled in NB in the Winter/Spring of 1999-2015. Statistical results from linear regression are shown on the figure, with linear trendline and 95% confidence intervals indicated by grey shading.

Table 2. 3 Results from linear regressions of sea-ice metrics (data from Stern and Laidre 2016) on different prey proportions in polar bear diet. Bears were sampled in the Winter/Spring in the Northern Beaufort Sea (NB) subpopulation, and the ice variables were lagged by a year, as most ice events [for the year] occurred after bear sampling. Bolded *p*-values indicate statistical significance.

	Spring break-up			**Fall freeze-up**			**Duration of open-water season**			**Summer sea-ice concentration**		
Prey	*F*-stat	R^2	*p*-value	*F*-stat	R^2	*p*-value	*F*-stat	R^2	*p*-value	*F*-stat	R^2	*p*-value
Subset: NB adult and subadult females												
Ringed Seal	0.688	0.071	0.428	0.515	-0.051	0.491	0.053	-0.105	0.822	0.209	-0.086	0.658
Beluga Whale	7.600	0.398	**0.022**	1.786	0.073	0.214	0.873	-0.013	0.374	1.019	0.002	0.339
Bowhead Whale	4.137	0.239	0.072	0.502	-0.-51	0.496	0.935	-0.007	0.359	0.375	-0.067	0.555
Bearded Seal	0.037	-0.107	0.852	0.019	-0.109	0.892	0.052	-0.105	0.825	0.324	-0.060	0.581
Subset: NB adult and subadult males												
Ringed Seal	0.659	-0.029	0.434	0.263	-0.065	0.619	0.105	-0.081	0.752	1.583	0.046	0.234
Beluga Whale	1.793	0.062	0.208	0.197	-0.072	0.666	0.517	-0.042	0.487	1.473	0.038	0.250
Bowhead Whale	2.459	0.108	0.145	2.632	0.120	0.133	0.079	-0.083	0.784	0.010	-0.090	0.921
Bearded Seal	0.297	-0.062	0.597	1.248	0.020	0.288	0.029	-0.088	0.867	0.017	-0.089	0.898

Sea ice dynamics were significantly related to the body condition of female polar bears in NB, where shorter duration of the open-water season and later dates of sea ice break-up were positively related to body condition (Fig. 2.16). Additionally, there was a non-significant positive trend between summer ice concentration and body condition, and no effect of the date of fall freeze-up on body condition (Fig. 2.16). Conversely, the body condition of male polar bears in NB was not affected by the summer ice concentration ($F_{1,11}$ = 0.385, R^2 = -0.054, p = 0.547), the duration of the open-water season ($F_{1,11}$ = 0.217, R^2 = -0.070, p = 0.650), the date of fall freeze-up ($F_{1,11}$ = 0.601, R^2 = -0.034, p = 0.455), or the date of spring break-up ($F_{1,11}$ = 0.004, R^2 = -0.091, p = 0.950).

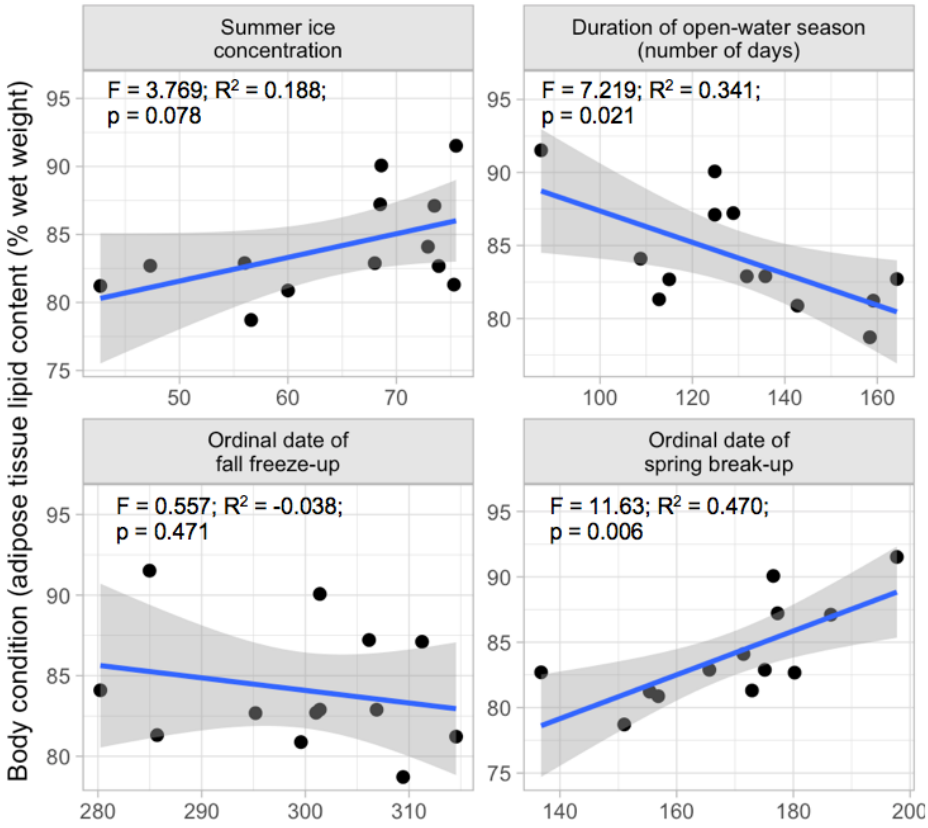

Figure 2. 16 The effect of sea ice conditions (data from Stern and Laidre (2016)) on body condition of female polar bears harvested in the Northern Beaufort Sea subpopulation from 1999-2015. Statistical results from linear regression are shown on the figure, with linear trendline and 95% confidence intervals indicated by grey shading.

Discussion

Polar bears are top predators reliant on sea ice, and their foraging habits can provide insights into the effects of climate change on the Arctic marine food web. These results provide novel insights in the relationship between sea ice conditions, polar bear diet, body condition, and variability in space, time, and age/sex in region undergoing rapid sea ice decline.

Fatty Acid Profiles

Polar bear FA profiles differed by subpopulation, season, age, and sex. These results are consistent with the differences in diet estimation among these groups, supporting the hypotheses that polar bear foraging is different across spatial and temporal scales, as well among demographic groups. This also supports my quantitative diet estimates, as they also differ between subpopulations, seasons, age classes, and sex.

The marine mammal species used in the QFASA prey library were well-separated from each other, making this prey library a reliable source to use for dietary studies. The most distinctly clustered prey species FA on the PCA plot was bearded seal, presumably due to the unique foraging patterns of bearded seals on benthic invertebrates (Thiemann et al. 2008b). Ringed seal and beluga whale feed upon pelagic fish (Loseto et al. 2009; Yurkowski et al. 2016b) possibly explaining the close clustering (Fig 2.2). Bowhead whales feed on copepods and euphausiids (Budge et al. 2008) and the similarity to beluga whale possibly reflects phylogenetic patterns. Regardless, in combination with the leave-one-prey-out diagnostics (R package: qfasar; Bromaghin 2017), this prey library was considered to be performing well in the fatty acid analyses.

Spatial Patterns

The longitude of harvest location explained the most variation in polar bear diet (Table 2.2), specifically for male adults and subadults. Male bears consumed relatively more bearded seal and bowhead whale in the west portion of the study area, and more beluga whale and ringed seal in the east (Fig. 2.6). These patterns may be consistent with prey abundance: bearded seals primarily reside in the offshore pack-ice and may be in greater abundance in the Beaufort and Chukchi Seas than the Amundsen Gulf (Smith 1980; Quakenbush et al. 2011), and a greater abundance of ringed seal is supported in the Amundsen Gulf than the Beaufort and Chukchi Seas (Harwood and Kingsley 2013; Pilfold et al. 2014; Harwood et al. 2015). Amundsen Gulf is also an important ringed seal pupping area (Harwood et al. 2000, 2012). Greater proportions of bowhead whale in the western portion of the study area is consistent with access to subsistence-harvested bowhead whale carcasses along the Alaskan coast (Ashjian et al. 2010; Herreman and Peacock 2013). This food source may be particularly useful for SB bears given the rate of sea ice decline in the region (Stern and Laidre 2016). Bears may have had access to beluga whales as they migrated from the Bering Sea to the Beaufort Sea in spring; whales move adjacent to the landfast ice in the Mackenzie Shelf and Amundsen Gulf in late May/early June (Harwood and Smith 2002), further aggregate in the Mackenzie Estuary when the landfast ice breaks up (Huntington et al. 1999; Harwood and Smith 2002; Luque and Ferguson 2009; Hornby et al. 2016) and disperse offshore across the Mackenzie Shelf in late July/August (Harwood and Kingsley 2013). My results suggest male polar bears consumed greater proportions of beluga whale in Amundsen Gulf than the western portion of the study area (i.e., Mackenzie Estuary), perhaps suggesting there are more polar bear foraging opportunities on beluga whale during their Mackenzie Estuary shoulder seasons. In contrast to adult males, female polar bears showed no spatial structure in their diet composition, possibly as a consequence of shared feeding areas,

such as around the Cape Bathurst Polynya (Thiemann et al. 2008a). Alternatively, female polar bears rely on ringed seal more than males, and may hunt ringed seal throughout the study area. My results of female foraging on ringed seals throughout the study area (Fig. 2.7) are consistent with kill-sites observed by Pilfold et al. (2014) who found ringed seal kill-sites along the landfast ice along the Tuktoyaktuk Peninsula Region, western Banks Island, and in the Amundsen Gulf.

Intraspecific Patterns

Polar bear diet was most heavily influenced by longitude, but also sex, age, age class, date of sea ice freeze-up and break-up, year, season, and the ordinal date of harvest (Table 2.2). Variability in polar bear diet between sexes and age classes may be due to differences in hunting ability, energetic requirements, and spatial segregation. My results are consistent with previous studies (e.g., Thiemann et al. 2008a) that suggest adult female polar bears are more reliant on ringed seals than are adult males, which forage more on bearded seals. Females with dependent cubs may focus their hunting on ringed seals on the land-fast ice, thus avoiding spatial overlap with potentially infanticidal adult male bears, which may hunt in the offshore pack ice where bearded seal densities are higher (Smith 1980; Quakenbush et al. 2011). The large size of adult male bears allows them to potentially hunt large-bodied prey, like adult bearded seals, more easily (Derocher et al. 2005, 2010). Solitary adult females, and subadult bears of both sexes, may have access to bearded seal pups and be able to scavenge on remains from adult bearded seal kills made by adult male polar bears.

I found males in NB consumed proportionately more bearded seal with age (Fig. 4), likely due to increasing body mass, as male polar bears continue to grow well after sexual maturity (Derocher et al. 2010). Thiemann et al. (2007) documented a positive correlation between adult male body mass and bearded seal consumption. The clear age-driven shift away

from ringed seal and towards bearded seal in male polar bears may serve to reduce intraspecific competition with adult females and juvenile bears, which are more dependent on ringed seal because of their smaller body size. I found no trend between age and diet in SB, possibly due to low sample sizes (Table 2.1), specifically with a limited number of older bears (Fig. 5).

Body Condition and Diet

Body condition, as inferred from adipose-tissue lipid content, was lower in SB than NB, which may be related to differences in sea-ice conditions, where ice is declining at a faster rate in SB than NB (Stern and Laidre 2016). Among SB female bears, body condition was positively correlated with the consumption of ringed seal and negatively correlated with beluga whale consumption (Fig. 2.11). These patterns suggest that female bears experience declining body condition when preferred ringed seal prey are less available, and rely more heavily on scavenging the carcasses of large bodied prey. The lack of relationship between body condition and diet in male bears may be a consequence of greater dietary flexibility in male bears and their ability to exploit bearded seals as a widely available prey. Similarly, the lack of relationship between diet composition and body condition of bears in NB may be related to superior habitat quality and higher or more predictable prey abundance, relative to SB where habitat conditions have declined dramatically in recent years (Fig. 2.14).

Seasonal and Interannual Trends

Seasonal differences in diet composition suggest that polar bears feed on seasonally available prey, particularly increased beluga whale consumption in the winter/spring. Predation on beluga whale is presumably related to the spatial trends in beluga consumption related to migration, which is dependent on sea-ice conditions (Huntington 2002; Hornby et al. 2016). Forecasted sea-

ice trends may allow for the timing of beluga migration to occur progressively earlier in the winter/spring providing an important food source for polar bears.

Diet composition varied across years for all age classes and sexes, suggesting interannual variation in prey availability. Adult and subadult females in NB appeared to consume more beluga whale in years when less ringed seal was consumed, and more ringed seal when beluga whale was reduced, while bowhead whale and bearded seal did not appear to be related to amount of ringed seal and beluga whale. My results suggest beluga whale is an important secondary prey source for both male and female polar bears in NB. The decline in ringed seal consumption for adult and subadult polar bears in 2007, and for just female subadults and adults in 2010 (Fig. 2.12), suggest there was possibly a decrease in ringed seals available in those years. Summer Arctic sea-ice extent was at a record minimum in 2007 (Wood et al. 2013); presumably decreasing the ability for ringed seals to build birth lairs and for polar bears to access ringed seals, decreasing the accessibility of this important food source. Low ringed seal consumption and low body condition of NB polar bears in 2007 is consistent with my hypothesis that reduced sea-ice would result in a decrease of polar bear foraging on ringed seals, and an increase in foraging more on alternative prey species, such as beluga whale (Fig. 2.12). Recent climatic shifts in the Arctic marine ecosystem, and particularly in the Beaufort Sea, such as increased upwelling of nutrients and an increase in pelagic marine productivity along the Beaufort slope (Schulze and Pickart 2012; Pickart et al. 2013), may offer favorable conditions for beluga whales providing a longer duration and a larger geographic area with access to food (Harwood and Kingsley 2013). More generally, Harwood and Kingsley (2013) report an increase in beluga whale abundance in the offshore Beaufort Sea in late August in recent years (2007-2009) relative to the mid-1980s.

Hornby et al. (2014) conducted beluga whale aerial surveys over the Mackenzie River estuary and the Tuktoyaktuk Peninsula from 2011-2013, and found relatively low abundance of beluga in 2011 (23 whales; possibly due to logistical effects of poor weather), higher abundance in 2012 (270 beluga observed on the day of ice break up; similar to surveys done in the 1970s and 1980s), and relatively high beluga density in 2013; the authors report 305 whales observed the day after ice break up in 2013. Here, I estimate beluga whale proportions in polar bear diet in the SB subpopulation were 19.2%, 21.4%, and 8.0% for females, and 28.2%, 23.7%, and 8.1% for males in 2011, 2012, and 2013, respectively. Estimated contribution of beluga whale to polar bear diets is not consistent with the relative counts from aerial surveys, suggesting that years with comparatively higher numbers of beluga in the Mackenzie River estuary and near the Tuktoyaktuk Peninsula are not necessarily years polar bears are able to forage on more beluga whale. It is possible that beluga whales are entering the Mackenzie River estuary in greater abundance earlier in the open water season, then seeking alternative foraging habitats offshore in late August. Overall, my results suggest higher consumption of beluga whale than previously documented among bears in the region (Thiemann et al. 2008a; Rode et al. 2014; McKinney et al. 2017).

Binned diet data for bears in SB differed across the three sampling periods: 2003-2006 (a period of population decline); 2007-2010 (when adult survival improved and the population stabilized; Bromaghin et al. 2015); and 2011-2014 (a period of unknown survival). My data, based on limited sample sizes, was not consistent with Bromaghin et al.'s (2015) hypothesis that low survival in 2004-2006 may have been due to limited access to prey or low prey abundance, at least for any particular prey species. Moreover, the lack of differences in body condition between periods of population decline (2003-2006) and stability (2007-2010) was not indicative

of a change in overall foraging success. However, the increase in bowhead whale consumption in 2007-2010, presumably from bears scavenging the carcasses of subsistence-harvested whales, may reflect increasing use of an anthropogenic food source during a period of low sea ice availability. The relatively low body condition of SB bears in the most recent period suggests that foraging success has not improved since the period of demographic decline in this subpopulation.

Sea-Ice

Sea-ice freeze-up occurred progressively later in the year, and subsequently the duration of the open water season increased over the study period (Fig. 2.14). However, these long-term declines in sea ice conditions were not matched by similar trends in polar bear diet composition in NB, which showed interannual variability that was not obviously driven by sea ice conditions. Similarly, sea ice and diet analyses were precluded by low sample sizes in SB, but binned diet data (Fig. 2.13) did not show any clear directional trends that would match sea ice decline. However, I found a significant positive correlation between date of sea ice break-up and proportion of beluga whale in the diet of female adult and subadult bears in NB, where later ice break-up was correlated with higher beluga whale consumption. Heavy spring ice conditions may delay beluga movements into and out of summer feeding areas, which may result in beluga entrapments during fall freeze-up in the southern Beaufort Sea (Higdon and Ferguson 2012). Thus, my results suggest spring sea ice conditions are a driver of beluga whale consumption, and are potentially indicative of polar bears foraging on beluga whales at entrapment events. Additionally, inconsistency between beluga whale consumption (Fig 2.12) and beluga whale abundance (Hornby et al. 2014) suggest the timing of ice break-up is more important than whale abundance for polar bear foraging. Furthermore, there was a positive relationship between date

of spring ice break-up and body condition of female bears in NB, suggesting that an increased amount of on-ice time in the spring, along with heavier beluga whale consumption, is linked to higher body condition. The negative relationship between duration of open-water season, and the near-significant negative relationship of summer ice concentration, and body condition also suggests on-ice foraging is essential for foraging success of female polar bears. In contrast to female bears, male bears had no relationships between sea ice conditions and body condition (or diet), possibly indicative of their flexible diet and ability to exploit larger-bodied prey.

Although the trend was not significant, I found evidence of reduced ringed seal consumption of NB bears in years with delayed sea ice break-up. Heavy spring sea ice conditions have reduced the reproductive success of Beaufort Sea ringed seals in the past (Stirling 2002) and may limit the ability of polar bears to prey on newly weaned ringed seal pups.

My results suggest polar bear foraging is variable across spatial, temporal, and intraspecific scales, possibly due to the local availability of prey species, in combination with differences in polar bear hunting ability. These results provide novel insights on the impact of spring sea ice break-up timing on polar bear diet and body condition in regions undergoing rapid reductions in sea ice. This information is essential for understanding how projected climatic declines in sea ice may further affect polar bear foraging and body condition, and ultimately the long-term ecological effects and conservation of Arctic marine mammals.

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Chapter 2: Supplementary Information

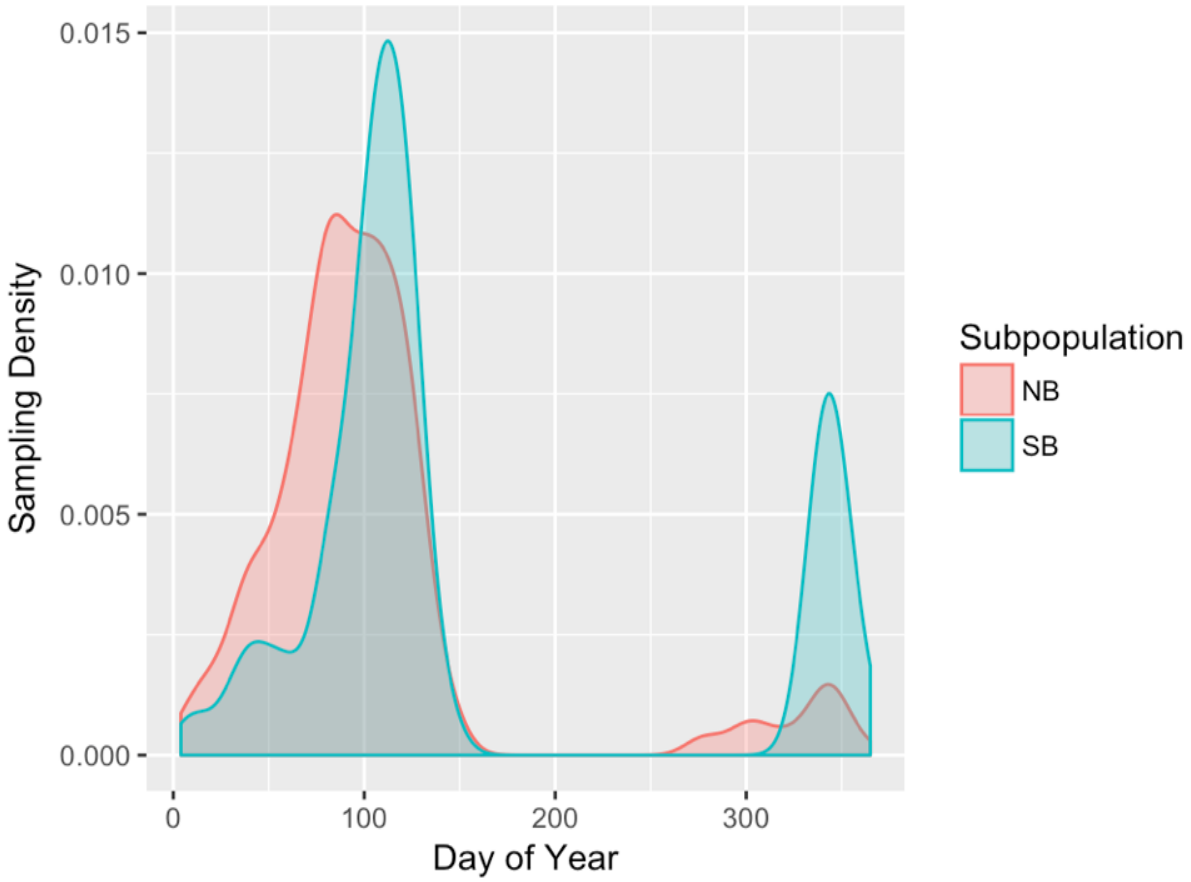

Figure S2. 1 Sampling density of polar bears throughout the year in the Northern Beaufort Sea (NB) and Southern Beaufort Sea (SB) subpopulations.

Table S2. 1 Fatty acids (mean ± SE) of 521 polar bears in the Northern Beaufort Sea and Southern Beaufort Sea subpopulation. * represents the subset FA used in dietary analyses; **bold** represents the FA used in the QFASA model analyses.

Fatty Acid	Northern Beaufort Sea n = 459	Southern Beaufort Sea n = 62
Saturated fat		
14:0*	2.752 ± 0.022	2.991 ± 0.067
Iso15	0.154 ± 0.002	0.163 ± 0.004
15:0	0.209 ± 0.003	0.226 ± 0.008
16:0*	5.535 ± 0.071	5.989 ± 0.189
7Me16:0	0.215 ± 0.003	0.238 ± 0.008
18:0	1.848 ± 0.043	1.999 ± 0.071
Monosaturated fat		
14:1n-5	0.712 ± 0.008	0.74 ± 0.024
16:1n-11	0.128 ± 0.004	0.135 ± 0.013
16:1n-9	0.546 ± 0.004	0.535 ± 0.011
16:1n-7*	13.303 ± 0.201	14.328 ± 0.6
17:1	0.248 ± 0.003	0.263 ± 0.007
18:1n-11	5.676 ± 0.087	5.227 ± 0.284
18:1n-9*	18.689 ± 0.158	18.496 ± 0.595
18:1n-7*	5.103 ± 0.052	5.41 ± 0.13
18:1n-5	0.485 ± 0.004	0.518 ± 0.01
20:1n-11	3.78 ± 0.059	3.385 ± 0.162
20:1n-9*	11.652 ± 0.167	10.331 ± 0.422
20:1n-7*	1.663 ± 0.035	1.512 ± 0.072
22:1n-11*	2.087 ± 0.041	1.989 ± 0.127
22:1n-9	0.906 ± 0.016	0.78 ± 0.043
22:1n-7*	0.143 ± 0.002	0.135 ± 0.007
Polyunsaturated fat		
16:2n-6*	0.039 ± 0.001	0.043 ± 0.002
16:2n-4*	0.133 ± 0.001	0.125 ± 0.004
16:3n-6*	0.415 ± 0.005	0.423 ± 0.016
16:3n-4*	0.089 ± 0.002	0.106 ± 0.01
16:4n-3*	0.051 ± 0.001	0.056 ± 0.004
16:4n-1*	0.053 ± 0.002	0.07 ± 0.007
18:2n-6*	1.055 ± 0.006	1.089 ± 0.02
18:3n-6*	0.096 ± 0.001	0.096 ± 0.004
18:3n-4*	0.2 ± 0.002	0.208 ± 0.004
18:3n-3*	0.338 ± 0.004	0.358 ± 0.012
18:3n-1*	0.058 ± 0.001	0.054 ± 0.002
18:4n-3*	0.314 ± 0.007	0.363 ± 0.025
18:4n-1*	0.106 ± 0.003	0.117 ± 0.008
20:2n-6*	0.26 ± 0.002	0.246 ± 0.005
20:3n-6*	0.146 ± 0.001	0.133 ± 0.003
20:4n-6*	0.252 ± 0.004	0.264 ± 0.012
20:3n-3*	0.047 ± 0.001	0.049 ± 0.002
20:4n-3*	0.31 ± 0.004	0.335 ± 0.012
20:5n-3*	2.357 ± 0.061	2.55 ± 0.211
21:5n-3*	0.29 ± 0.003	0.315 ± 0.01
22:4n-6*	0.157 ± 0.004	0.146 ± 0.007
22:5n-6*	0.175 ± 0.003	0.184 ± 0.006
22:4n-3*	0.079 ± 0.001	0.092 ± 0.006
22:5n-3*	7.09 ± 0.057	7.178 ± 0.19
22:6n-3*	8.36 ± 0.1	8.243 ± 0.281

Table S2. 2 Sex differences in mean (± SE) fatty acid values from 505 polar bears in the Beaufort Sea. * represents the subset FA used in dietary analyses; **bold** represents the FA used in the QFASA model analyses. (note: the sex of 16 bears were unknown)

Fatty Acid	Females n = 174	Males n = 331
Saturated fat		
14:0*	2.787 ± 0.037	2.773 ± 0.026
Iso15	0.152 ± 0.003	0.156 ± 0.002
15:0	0.195 ± 0.004	0.218 ± 0.004
16:0*	5.275 ± 0.095	5.738 ± 0.089
7Me16:0	0.223 ± 0.005	0.214 ± 0.003
18:0	1.618 ± 0.026	1.993 ± 0.056
Monosaturated fat		
14:1n-5	0.748 ± 0.013	0.7 ± 0.009
16:1n-11	0.136 ± 0.007	0.126 ± 0.004
16:1n-9	0.557 ± 0.006	0.537 ± 0.005
16:1n-7*	13.092 ± 0.282	13.585 ± 0.251
17:1	0.233 ± 0.004	0.259 ± 0.004
18:1n-11	5.873 ± 0.122	5.482 ± 0.11
18:1n-9*	18.724 ± 0.264	18.594 ± 0.191
18:1n-7*	4.796 ± 0.051	5.306 ± 0.067
18:1n-5	0.509 ± 0.005	0.478 ± 0.004
20:1n-11	3.677 ± 0.081	3.765 ± 0.074
20:1n-9*	12.142 ± 0.223	11.166 ± 0.206
20:1n-7*	1.336 ± 0.022	1.807 ± 0.045
22:1n-11*	2.163 ± 0.06	2.037 ± 0.051
22:1n-9	0.909 ± 0.022	0.885 ± 0.02
22:1n-7*	0.14 ± 0.003	0.143 ± 0.003
Polyunsaturated fat		
16:2n-6*	0.04 ± 0.001	0.039 ± 0.001
16:2n-4*	0.134 ± 0.002	0.132 ± 0.001
16:3n-6*	0.426 ± 0.007	0.411 ± 0.006
16:3n-4*	0.09 ± 0.004	0.091 ± 0.003
16:4n-3*	0.05 ± 0.002	0.052 ± 0.002
16:4n-1*	0.055 ± 0.003	0.055 ± 0.002
18:2n-6*	1.052 ± 0.011	1.063 ± 0.007
18:3n-6*	0.097 ± 0.002	0.096 ± 0.001
18:3n-4*	0.189 ± 0.002	0.207 ± 0.002
18:3n-3*	0.351 ± 0.005	0.335 ± 0.005
18:3n-1*	0.056 ± 0.001	0.058 ± 0.001
18:4n-3*	0.327 ± 0.011	0.317 ± 0.008
18:4n-1*	0.104 ± 0.004	0.109 ± 0.003
20:2n-6*	0.243 ± 0.002	0.267 ± 0.003
20:3n-6*	0.138 ± 0.002	0.149 ± 0.002
20:4n-6*	0.229 ± 0.005	0.266 ± 0.006
20:3n-3*	0.048 ± 0.001	0.046 ± 0.001
20:4n-3*	0.312 ± 0.005	0.313 ± 0.005
20:5n-3*	2.416 ± 0.099	2.367 ± 0.074
21:5n-3*	0.288 ± 0.004	0.297 ± 0.004
22:4n-6*	0.134 ± 0.004	0.167 ± 0.005
22:5n-6*	0.162 ± 0.003	0.185 ± 0.004
22:4n-3*	0.081 ± 0.002	0.08 ± 0.002
22:5n-3*	7.22 ± 0.095	7.062 ± 0.065
22:6n-3*	8.906 ± 0.143	8.098 ± 0.119

Table S2. 3 Fatty acid (mean ± SE) of 472 polar bears in the Beaufort Sea, including 2 year olds, subadults (3-4 years old), and adults (5+ years old). * represents the subset FA used in dietary analyses; **bold** represents the FA used in the QFASA model analyses. (note: the age of 49 bears were unknown).

Fatty Acid	2 year old n = 49	Subadults n = 172	Adults n = 251
Saturated fat			
14:0*	2.955 ± 0.07	2.839 ± 0.036	2.702 ± 0.028
Iso15	0.158 ± 0.004	0.156 ± 0.003	0.153 ± 0.002
15:0	0.215 ± 0.009	0.209 ± 0.004	0.211 ± 0.004
16:0*	5.778 ± 0.246	5.603 ± 0.109	5.536 ± 0.09
7Me16:0	0.231 ± 0.008	0.226 ± 0.004	0.209 ± 0.004
18:0	1.871 ± 0.134	1.844 ± 0.089	1.878 ± 0.029
Monosaturated fat			
14:1n-5	0.77 ± 0.023	0.754 ± 0.013	0.678 ± 0.01
16:1n-11	0.124 ± 0.009	0.142 ± 0.007	0.121 ± 0.004
16:1n-9	0.557 ± 0.012	0.556 ± 0.006	0.534 ± 0.005
16:1n-7*	13.489 ± 0.481	13.282 ± 0.269	13.498 ± 0.294
17:1	0.243 ± 0.008	0.241 ± 0.004	0.258 ± 0.004
18:1n-11	5.408 ± 0.196	5.819 ± 0.132	5.535 ± 0.123
18:1n-9*	18.623 ± 0.438	18.598 ± 0.257	18.723 ± 0.217
18:1n-7*	4.86 ± 0.117	4.87 ± 0.058	5.377 ± 0.077
18:1n-5	0.511 ± 0.011	0.503 ± 0.005	0.475 ± 0.005
20:1n-11	3.49 ± 0.148	3.543 ± 0.081	3.916 ± 0.082
20:1n-9*	11.297 ± 0.402	11.445 ± 0.233	11.584 ± 0.235
20:1n-7*	1.343 ± 0.044	1.356 ± 0.027	1.904 ± 0.052
22:1n-11*	1.997 ± 0.109	2.127 ± 0.068	2.057 ± 0.054
22:1n-9	0.855 ± 0.036	0.877 ± 0.024	0.91 ± 0.022
22:1n-7*	0.133 ± 0.005	0.138 ± 0.004	0.146 ± 0.003
Polyunsaturated fat			
16:2n-6*	0.042 ± 0.002	0.041 ± 0.001	0.038 ± 0.001
16:2n-4*	0.136 ± 0.004	0.133 ± 0.002	0.131 ± 0.001
16:3n-6*	0.436 ± 0.015	0.426 ± 0.007	0.405 ± 0.006
16:3n-4*	0.109 ± 0.008	0.094 ± 0.004	0.085 ± 0.003
16:4n-3*	0.052 ± 0.004	0.055 ± 0.002	0.049 ± 0.002
16:4n-1*	0.065 ± 0.007	0.058 ± 0.003	0.051 ± 0.002
18:2n-6*	1.025 ± 0.021	1.041 ± 0.01	1.078 ± 0.007
18:3n-6*	0.099 ± 0.004	0.098 ± 0.002	0.094 ± 0.002
18:3n-4*	0.192 ± 0.006	0.19 ± 0.002	0.21 ± 0.003
18:3n-3*	0.343 ± 0.011	0.351 ± 0.006	0.332 ± 0.005
18:3n-1*	0.058 ± 0.001	0.055 ± 0.001	0.059 ± 0.001
18:4n-3*	0.352 ± 0.022	0.343 ± 0.011	0.297 ± 0.008
18:4n-1*	0.113 ± 0.01	0.107 ± 0.004	0.106 ± 0.004
20:2n-6*	0.245 ± 0.006	0.242 ± 0.002	0.272 ± 0.003
20:3n-6*	0.141 ± 0.005	0.138 ± 0.002	0.15 ± 0.002
20:4n-6*	0.266 ± 0.014	0.25 ± 0.007	0.254 ± 0.006
20:3n-3*	0.046 ± 0.001	0.048 ± 0.001	0.046 ± 0.001
20:4n-3*	0.307 ± 0.012	0.314 ± 0.005	0.312 ± 0.005
20:5n-3*	2.723 ± 0.192	2.602 ± 0.099	2.158 ± 0.078
21:5n-3*	0.29 ± 0.008	0.291 ± 0.005	0.295 ± 0.005
22:4n-6*	0.136 ± 0.007	0.132 ± 0.003	0.176 ± 0.006
22:5n-6*	0.163 ± 0.006	0.159 ± 0.003	0.191 ± 0.004
22:4n-3*	0.084 ± 0.006	0.079 ± 0.001	0.081 ± 0.002
22:5n-3*	6.987 ± 0.192	7.063 ± 0.085	7.147 ± 0.075
22:6n-3*	8.999 ± 0.308	8.952 ± 0.146	7.803 ± 0.125

Table S2. 4 Fatty acid composition (mean ± SE) of prey (n = 447) used in QFASA analyses. Data from Bromaghin et al. (2015). * represents the subset FA used in dietary analyses; **bold** represents the FA used in the QFASA model analyses.

Fatty Acid	Bearded Seal n = 82	Beluga Whale n = 29	Bowhead Whale n = 64	Ringed Seal n = 272
Saturated fat				
14:0*	2.891 ± 0.06	6.434 ± 0.12	4.322 ± 0.045	3.008 ± 0.04
Iso15	0.124 ± 0.003	0.62 ± 0.043	0.119 ± 0.001	0.126 ± 0.001
15:0	0.382 ± 0.007	0.304 ± 0.007	0.24 ± 0.002	0.174 ± 0.003
16:0*	9.064 ± 0.177	6.641 ± 0.201	10.144 ± 0.166	4.263 ± 0.084
7Me16:0	0.293 ± 0.004	0.342 ± 0.007	0.256 ± 0.003	0.268 ± 0.004
18:0	1.43 ± 0.039	0.948 ± 0.055	2.203 ± 0.051	0.552 ± 0.011
Monosaturated fat				
14:1n-5	0.768 ± 0.036	2.133 ± 0.207	0.42 ± 0.01	1.278 ± 0.022
16:1n-11	0.431 ± 0.009	1.403 ± 0.087	0.405 ± 0.004	0.332 ± 0.014
16:1n-9	0.329 ± 0.004	1.335 ± 0.088	0.222 ± 0.003	0.552 ± 0.009
16:1n-7*	20.533 ± 0.318	22.621 ± 0.928	17.299 ± 0.19	18.096 ± 0.222
17:1	0.591 ± 0.012	0.243 ± 0.012	0.179 ± 0.004	0.208 ± 0.005
18:1n-11	0.532 ± 0.034	3.693 ± 0.131	2.365 ± 0.077	3.833 ± 0.087
18:1n-9*	15.708 ± 0.266	13.341 ± 0.342	12.577 ± 0.252	13.792 ± 0.142
18:1n-7*	9.323 ± 0.17	3.336 ± 0.08	5.077 ± 0.071	3.939 ± 0.057
18:1n-5	0.58 ± 0.01	0.44 ± 0.019	0.602 ± 0.006	0.515 ± 0.006
20:1n-11	1.852 ± 0.101	3.933 ± 0.175	2.178 ± 0.061	1.835 ± 0.047
20:1n-9*	2.133 ± 0.095	7.463 ± 0.473	9.213 ± 0.242	8.031 ± 0.176
20:1n-7*	2.305 ± 0.082	0.644 ± 0.055	1.51 ± 0.038	0.836 ± 0.025
22:1n-11*	0.417 ± 0.038	4.892 ± 0.451	5.236 ± 0.189	1.197 ± 0.044
22:1n-9	0.166 ± 0.01	1.001 ± 0.109	1.182 ± 0.043	0.561 ± 0.018
22:1n-7*	0.078 ± 0.005	0.199 ± 0.025	0.277 ± 0.009	0.104 ± 0.003
Polyunsaturated fat				
16:2n-6*	0.768 ± 0.001	0.085 ± 0.002	0.067 ± 0.002	0.072 ± 0.001
16:2n-4*	0.431 ± 0.007	0.267 ± 0.008	0.037 ± 0.001	0.174 ± 0.003
16:3n-6*	0.329 ± 0.007	0.738 ± 0.017	0.702 ± 0.005	0.718 ± 0.008
16:3n-4*	20.533 ± 0.006	0.185 ± 0.006	0.221 ± 0.007	0.315 ± 0.009
16:4n-3*	0.591 ± 0.004	0.068 ± 0.002	0.076 ± 0.001	0.087 ± 0.002
16:4n-1*	0.532 ± 0.012	0.191 ± 0.01	0.319 ± 0.013	0.333 ± 0.013
18:2n-6*	15.708 ± 0.015	0.734 ± 0.016	0.662 ± 0.006	0.883 ± 0.008
18:3n-6*	9.323 ± 0.003	0.068 ± 0.003	0.135 ± 0.002	0.175 ± 0.005
18:3n-4*	0.58 ± 0.005	0.07 ± 0.007	0.26 ± 0.004	0.141 ± 0.003
18:3n-3*	1.852 ± 0.012	0.273 ± 0.009	0.333 ± 0.005	0.478 ± 0.005
18:3n-1*	2.133 ± 0.003	0.055 ± 0.004	0.037 ± 0.001	0.053 ± 0.002
18:4n-3*	2.305 ± 0.019	0.357 ± 0.017	0.699 ± 0.021	0.913 ± 0.019
18:4n-1*	0.417 ± 0.008	0.108 ± 0.005	0.43 ± 0.009	0.133 ± 0.002
20:2n-6*	0.166 ± 0.008	0.113 ± 0.006	0.158 ± 0.002	0.196 ± 0.004
20:3n-6*	0.078 ± 0.003	0.057 ± 0.003	0.07 ± 0.001	0.122 ± 0.003
20:4n-6*	0.768 ± 0.026	0.243 ± 0.008	0.302 ± 0.005	0.384 ± 0.01
20:3n-3*	0.431 ± 0.001	0.021 ± 0.001	0.038 ± 0.001	0.067 ± 0.001
20:4n-3*	0.329 ± 0.008	0.293 ± 0.012	0.444 ± 0.005	0.418 ± 0.004
20:5n-3*	20.533 ± 0.189	3.133 ± 0.152	9.153 ± 0.157	8.506 ± 0.115
21:5n-3*	0.591 ± 0.011	0.13 ± 0.008	0.372 ± 0.005	0.441 ± 0.006
22:4n-6*	0.532 ± 0.007	0.037 ± 0.002	0.025 ± 0.001	0.122 ± 0.003
22:5n-6*	15.708 ± 0.007	0.059 ± 0.003	0.058 ± 0.001	0.167 ± 0.003
22:4n-3*	9.323 ± 0.001	0.033 ± 0.003	0.06 ± 0.004	0.099 ± 0.002
22:5n-3*	0.58 ± 0.085	1.801 ± 0.125	3.152 ± 0.039	7.328 ± 0.072
22:6n-3*	1.852 ± 0.13	4.543 ± 0.27	4.641 ± 0.054	12.684 ± 0.136

Table S2. 5 Principal component (PC) scores for the first two axes of principal component analyses on the fatty acids of polar bears in the Northern Beaufort Sea (NB) and the Southern Beaufort Sea (SB).

Classification	PC1			PC2		
Subpopulation						
SB	0.300	±	2.307	-0.412	±	1.199
NB	-0.038	±	1.968	0.052	±	1.203
Age class						
Adults	0.270	±	1.777	0.067	±	1.218
Subadults	-0.315	±	2.212	-0.065	±	1.182
2 Year Old	-0.272	±	2.214	-0.114	±	1.271
Sex						
Females	-0.591	±	1.579	0.271	±	0.916
Males	0.296	±	2.143	-0.134	±	1.319

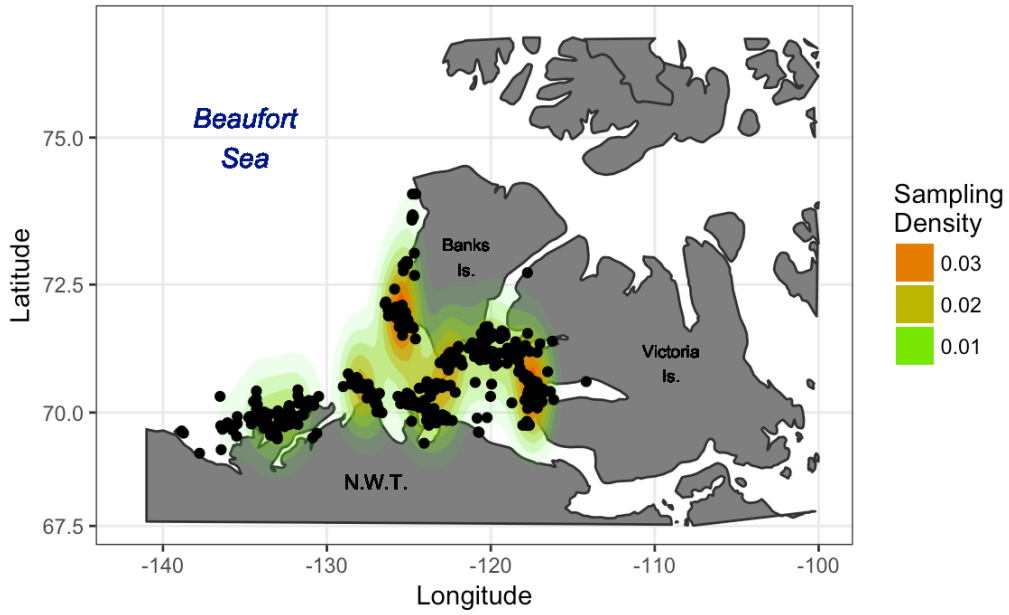

Figure S2. 2 Sampling density of all polar bears in the study from 1999 to 2015.

Chapter 3: Polar bear (*Ursus maritimus*) diet composition, body condition, and long-term sea ice trends in Viscount Melville Sound

Abstract

Rapid declines in Arctic sea ice has resulted in habitat loss for ice-dependent species. Polar bears (*Ursus maritimus*) are apex predators that rely on annual sea ice as their primary habitat for hunting marine mammal prey. Declines in sea ice have been linked to reduced polar bear body condition, reproduction, survival, and abundance. Although the precise demographic effects of sea ice loss on local polar bear populations are difficult to predict, they will likely be mediated by changes in foraging opportunities. I characterized the diet composition of polar bears in the Viscount Melville Sound subpopulation, where little is known about polar bear ecology but where significant declines in sea ice conditions have occurred over the past 30 years. I used quantitative fatty acid signature analysis to estimate the diets of 38 polar bears handled or harvested from 2012 to 2014. I also examined trends in sea ice extent since 1979 to characterize long term habitat conditions in the region. I found no differences in prey consumption between male and female bears, and I found adults consumed proportionately more bearded seal and less bowhead whale than younger conspecifics (i.e., ≤ 4 years old). I used adipose tissue lipid content as an index of body condition and found that male polar bears had a negative relationship between bearded seal consumption and body condition, possibly due to lack of available alternative prey. Bears ate less beluga whale in 2014 than 2012/2013, possibly due to heavy sea ice conditions and shorter open water duration in the year prior (2013) which restricted polar bear access to beluga whale. Declining sea ice conditions were associated with reduced consumption of preferred prey (i.e., ringed seal) and declining body condition, especially in female bears. My results provide the first diet estimates for polar bears in Viscount Melville

Sound and indicate that bears in this region rely more heavily on beluga whale than any other group of polar bears studied to date. These results, combined with extensive sea ice loss in the region over the past 30 years, suggest that the availability of preferred prey (i.e., ringed seals) is relatively low. It seems likely that ongoing changes in sea ice conditions will affect the availability of polar bear prey and my results can serve as an essential baseline against which future changes can be measured.

Introduction

Ecosystem change can affect the movement, distribution, and foraging ecology of wildlife (Paine 1966; Bowen 1997; Wilmers and Getz 2005; Hazen et al. 2012). Climate-driven changes in the Arctic ecosystem have caused sea ice extent (Stroeve et al. 2012), thickness (Lindsay and Schweiger 2015), and seasonal duration (Wang and Overland 2015) to decline at greater-than-forecasted rates (Stroeve et al. 2012). The presence of sea ice is a fundamental characteristic of Arctic marine ecosystems and declines in sea ice conditions can have dramatic effects on the ecology and distribution of marine species. For example, warmer sea surface temperatures and progressively earlier date of sea ice breakup has been linked to increased Arctic cod (*Boreogadus saida*) recruitment (Bouchard et al. 2017) and reduced ice cover may allow killer whales (*Orcinus orca*) to travel farther and remain longer in Arctic waters (Higdon and Ferguson 2009). Such ecological changes may lead to altered food web interactions. The foraging habits of top predators can thus reveal underlying ecological changes that are otherwise difficult to detect, especially in the early stages (Boyd and Murray 2001).

Polar bears (*Ursus maritimus*) are apex predators with a large spatial distribution and rely on sea ice as a platform for hunting, travelling, and mating (Stirling and Derocher 1993; Amstrup 2003; Durner et al. 2017; Lone et al. 2017; Togunov et al. 2017), making them a useful indicator

of ecological change (Iverson et al. 2006). Reductions in sea ice have been linked to declines in polar bear survival (Regehr et al. 2007; Rode et al. 2012), body condition (Derocher et al. 2004; Rode et al. 2010, 2012; Obbard et al. 2016; Sciullo et al. 2016), and reproduction (Rode et al. 2010). Concurrently, their primary prey, ringed seal (*Pusa hispida*), also rely on sea ice for recruitment and survival (Kingsley et al. 1985; Ferguson et al. 2005), and progressively earlier spring sea ice retreat has been linked to declines in ringed seal body condition (Harwood et al. 2012; Ferguson et al. 2017).

Besides ringed seals, polar bears prey on a variety of marine mammals across their circumpolar range (Derocher et al. 2002; Thiemann et al. 2008; Galicia et al. 2016; Sciullo et al. 2017). Polar bears may exhibit age- and sex-specific foraging patterns due to the effects of size and experience on hunting ability. Juveniles and adult females, which are approximately half the size of adult males (Derocher et al. 2005, 2010), are potentially restricted to hunting smaller-bodied species (e.g., ringed seals; Thiemann et al. 2008) or scavenging the carcasses of larger prey. Spatial segregation may also lead to age and sex-specific foraging as females attempt to avoid infanticide by adult males (Derocher and Wiig 1999); females with cubs may spend more time foraging on the land-fast ice where ringed seals are more abundant, while adult males and solitary females hunt in offshore pack ice with higher densities of bearded seals (Stirling et al. 1993). Adult males are presumably more capable than smaller conspecifics to adjust their foraging patterns to match local fluctuations in prey (Thiemann et al. 2011).

Several methods have been used to characterize predator diets, including analysing scat (Dellinger and Trillmich 1988), stomach contents (Hyslop 1980), and kill-site remains (i.e., Davidson et al. 2013). These methods are useful when used opportunistically, but unless done regularly on an individual predator, they may not accurately reflect diet over ecologically

relevant timescales. Fatty acid (FA) analyses provide insights into a mammalian predator's diet that integrate weeks to months of feeding before the date of sampling (Brockerhoff et al. 1967; Iverson et al. 2004). The relative proportions of FA in a consumer's adipose tissue (i.e., its FA "profile" or "signature") is a function of both diet and endogenous processes (Ackman and Eaton 1966; Iverson et al. 2004; Budge et al. 2006; Thiemann et al. 2008a). Diet composition of individual predators can be estimated using quantitative fatty acid signature analysis (QFASA; Iverson et al. 2004; Budge et al. 2006; Bromaghin 2017), which models the predator FA profile as a linear combination of potential prey signatures and determines the relative proportions of prey that comes closest to matching each observed predator signature, after accounting for FA-specific patterns of metabolism (Iverson et al. 2004).

Polar bears store energy in adipose tissue, and when energy is mobilized the relative proportion of lipid to non-lipid components declines (Pond 1992), hence, percent lipid in the adipose tissue is indicative of body condition (Thiemann et al. 2006; Sciullo et al. 2016). In Chapter 2, I found body condition positively correlated with female bears ringed seal consumption in the Southern Beaufort Sea subpopulation, and negatively correlated with male consumption of beluga whale.

Little is known about the Viscount Melville Sound Arctic-marine food web, and more specifically, the natural history and diet of polar bears in the region. My objectives were to (1) use QFASA to provide the first quantitative estimates of diet for polar bears in Viscount Melville Sound, from 2012 to 2014, (2) compare diet estimates to body condition, (3) examine long-term temporal trends in sea ice conditions within the Viscount Melville Sound subpopulation, and (4) compare recent sea ice conditions to polar bear diet composition. I predicted that polar bear diet composition and body condition would be affected by the availability of sea ice. I further

hypothesized that polar bear diets would differ with age and sex and that adults, specifically males, would consume greater proportions of bearded seal and beluga whale than females and subadults. This study provides essential data on the structure and functioning of the Viscount Melville Sound food web, and the ecological role of top predators in a region undergoing rapid sea ice loss.

Methods

Sample Collection

We collected adipose tissue samples from 38 polar bears harvested or captured in the Viscount Melville Sound subpopulation during April and May from 2012 to 2014 (Fig 3.1; Table 3.1). Bears caught <10 km outside of the Viscount Melville Sound boundary (Fig. 3.1) were included in analyses as polar bears have large home ranges (McCall et al. 2015; Auger-Méthé et al. 2016) and all captured bears were handled as part of a mark-recapture survey of the Viscount Melville Sound subpopulation. Free-ranging polar bears were located by helicopter and immobilized via remote injection of tiletamine HCl and zolazepam HCl (Zoletil®, Laboratories Virbac, Carros, France) following standard chemical immobilization protocols (Stirling et al. 1989). A unique identification number was tattooed on the inside of the upper lip and engraved on plastic ear tags. Adipose tissue samples were taken from 15 cm lateral to the base of the tail using a 6 mm biopsy punch, and consisted of a full-layer core from skin to muscle (Thiemann et al. 2006). Biopsy samples (approx. 0.3 g) were placed in a 2 ml vial and stored at –20°C until laboratory analyses. All immobilization and live-capture procedures were reviewed and approved by the Environment Canada Prairie and Northern Region Animal Care Committee. In addition to live-captures, samples were collected from 7 polar bears harvested by Inuvialuit hunters during annual subsistence hunts. Subcutaneous adipose tissue samples (approx. 8 cm x 4cm) were collected

from the rump of each bear and individually wrapped in aluminum foil, sealed in a Whirl-Pak, and stored at –20°C until laboratory analyses. The age of independent bears was determined by counting growth layer groups in the cementum of an extracted vestigial premolar tooth (Calvert and Ramsay 1998); bears were classified as adult (≥5 years), subadults (3-4 years), 2-year-olds, and yearlings.

Table 3. 1 Age and sex distribution of polar bears captured or harvested in the Viscount Melville Sound subpopulation. Bears were classified as adult (≥5 years), subadult (3-4 years), 2-year-old, or yearling.

Year	Total no. samples	Adult		Subadult		2-year old		Yearling	
		Female	Male	Female	Male	Female	Male	Female	Male
2012	**12**	5	1	1	3	0	0	1	1
2013	**10**	3	6	0	0	0	1	0	0
2014	**16**	9	5	1	0	1	0	0	0
Total	**38**	**17**	**12**	**2**	**3**	**1**	**1**	**1**	**1**

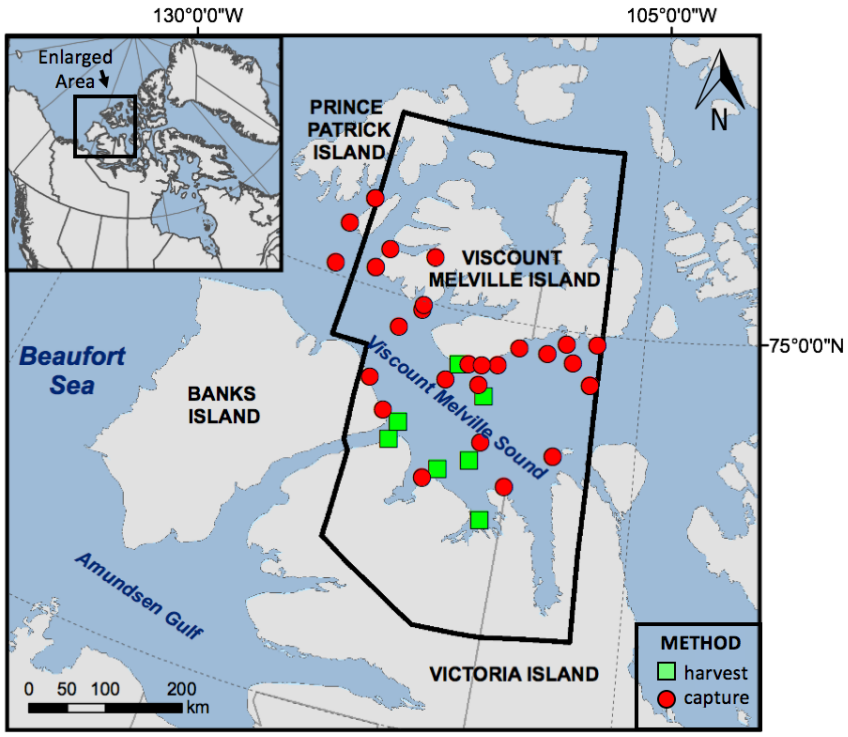

Figure 3. 1 Locations of polar bears harvested or live-captured in the Viscount Melville Sound subpopulation (boundary lines in black) from 2012-2014.

Laboratory Analyses

Polar bear harvest samples were subsampled (approx. 0.3 g), removing any surfaces that might be oxidized, and biopsy samples were used in full. Marine mammal prey samples were subsampled in full vertical depth due to stratification of pinniped and cetacean blubber (Budge et al. 2006; Strandberg et al. 2008). Lipid from each sample was quantitatively extracted and isolated using a modified Folch extraction (Folch et al. 1957; Iverson et al. 2001). FA methyl esters (FAME) were derived from the lipid extracts using sulfuric acid as a catalyst (Thiemann et al. 2004; Budge et al. 2006), and temperature-programmed gas chromatography (GC) was used to identify and analyze FAME in duplicate (Budge et al. 2006). The GC was used with a flame ionization detector fitted with a polar column (30 m x 0.25 mm inner diameter; DB-23; Agilent Technologies, Palo Alto, California, USA; Budge et al. 2006). I measured FA as mass-percent of total FA ± 1 standard error of the mean, and expressed each FA by the standard FA nomenclature of *A*:*B*n-*X*, where *A* is the length of the carbon chain, *B* is the number of double bonds, and *X* is the location of the double bond closest to the terminal methyl group. FA identifications were verified and manually corrected using CompassCDS software (Version 3.0, Bruker Daltonics Inc., Germany).

Diet Estimation

I used quantitative fatty acid signature analysis (QFASA; Iverson et al. 2004) to estimate the diets of individual polar bears. QFASA models the FA signature of each predator as a linear combination of potential prey and estimates diet composition as the proportions of prey that minimize the Aitchison distance between the modelled and observed predator signature. I used the prey FA library from Bromaghin et al. (2015; https://alaska.usgs.gov/products/data.php?dataid=44), who used QFASA to estimate the diets of

polar bears in the Chukchi Sea. Previous studies have demonstrated that species-specific differences in the FA profiles of Arctic marine mammals are considerably larger than regional differences (e.g., Thiemann et al. 2008b), so I am confident these prey FA values are applicable to the VM region, where few marine mammal samples are available. The prey database included 82 bearded seals, 29 beluga whales, 64 bowhead whales, and 222 ringed seals; I analyzed adipose tissue samples from an additional 50 ringed seals harvested in Amundsen Gulf (see Chapter 2), contributing to a total prey library of 447 animals. To account for FA-specific patterns of metabolism in the predator, I used calibration coefficients derived from captive mink (*Neovison vison*; Thiemann et al. 2008). Finally, I used a suite of 29 FA based on the set of Galicia et al. (2015) but excluding FA 22:1n-9 which I found contributed to confounding between prey types (see Chapter 2). QFASA diet estimations were computed in R (version 3.4.0, GUI 1.40, R Development Team 2017) using the *est_diet* function in the *qfasar* package (Bromaghin 2017).

Sea Ice Data

Sea ice data were extracted from the National Snow and Ice Data Centre database (NSIDC, Boulder, CO, http://nsidc.org/) from three satellites covering various time periods at different resolutions: (1) Nimbus-7 Scanning Multichannel Microwave (SMM) Radiometer and Defense Meteorological Satellite Program (DMSP) SSM Imager – SSM Imager/Sounder Passive Microwave Data (Cavalieri et al. 1996; daily coverage at 25 km x 25 km), (2) Advanced Microwave Scanning Radiometer – Earth Observing System (AMSR-E; for daily coverage at 12.5 km by 12.5 km from 2002 - 2011), and (3) Advanced Microwave Scanning Radiometer 2 for finest resolution (AMSR2; for daily coverage at 6 km by 6 km from 2012 to present). Data

were extracted within the Viscount Melville Sound polar bear subpopulation boundaries (Obbard et al. 2010).

I assessed long-term (1979-2014) temporal trends in four sea ice metrics: (1) date of sea ice retreat, (2) date of sea ice advance, (3) duration of the open-water season, and (4) mean summer sea ice concentration. Sea ice retreat and advance dates were determined for each year following the methods of Stern and Laidre (2016). Briefly, the mid-point between the March mean sea ice concentration and the September mean sea ice concentration was determined as the threshold value for each year. The day of the year that sea ice concentration crossed below or above the threshold was considered the date of sea ice retreat or sea ice advance, respectively. The duration of the open-water season was calculated as the number of days between sea ice retreat and sea ice advance, and the mean summer sea ice concentration was calculated across the Viscount Melville Sound subpopulation zone between June 1 and October 31.

Statistical Analyses

I used Mann-Whitney-Wilcoxon tests to compare the proportional consumption of prey species in polar bear diets, as the proportional data were not normally distributed. I used *t*-tests to investigate differences in individual prey species between sexes or age classes (i.e., adult vs. juvenile); Shapiro-Wilk tests were performed and data were normalized using square-root transformations if necessary. I used permutation analysis of variance (ANOVA) to test for year effects on each prey species separately. I used Spearman's rank correlation to test for correlations between polar bear diet (i.e., proportion of each prey type) and body condition (i.e., percent lipid in the adipose tissue).

I used linear regression to investigate long-term trends in the four sea ice variables. Sea ice variables were expected to covary, thus each variable was tested independently as a response

variable in the four separate regressions. Shapiro-Wilk tests were used to investigate variable normality, and square-root transformations were computed when necessary. Spearman correlations were used when sea ice variables were not normally distributed after transformations.

Due to constraints on sample size and study duration, sea ice metrics were qualitatively compared to polar bear diet estimates. Because bears were sampled in April/May, the date of sea ice retreat and advance, duration of the open water season, and mean sea ice concentration Jun-Oct had not occurred at the time of sample collection, thus, the previous year's sea ice metric was used in comparisons. All statistical analyses were conducted using R (version 3.4.2, GUI 1.70, R Development Team 2017).

Results

Diet Estimation

The mean diet of polar bears in the Viscount Melville Sound subpopulation across all age classes, sexes, and years was 45.0% ringed seal, 36.7% beluga whale, 11.1% bowhead whale, and 7.1% bearded seal (Fig. 3.2).

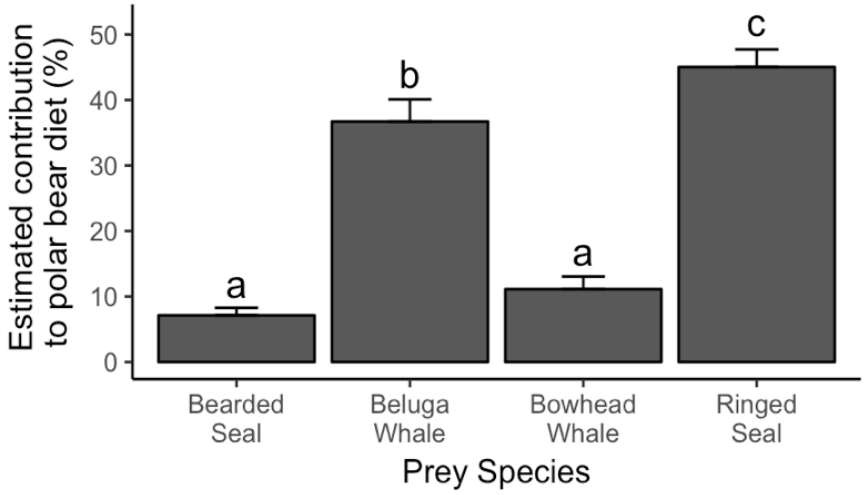

Figure 3. 2 Diet estimates (mean + SE) of polar bears in the Viscount Melville Sound subpopulation from 2011 to 2014. Statistical differences (Mann-Whitney-Wilcoxon tests) between prey species proportions are indicated by different letters.

Adult bears had a higher proportion of bearded seal (t = 2.54, df = 14.57, p = 0.023), and a lower proportion of bowhead whale (t = -2.43, df = 17.06, p = 0.026) in their diets than juvenile bears (Fig. 3.3). There was no difference between adult and juvenile bears in the amount of beluga whale (t = 1.78, df = 23.94, p = 0.087) or ringed seal (t = -1.35, df = 14.90, p = 0.196) in their diets.

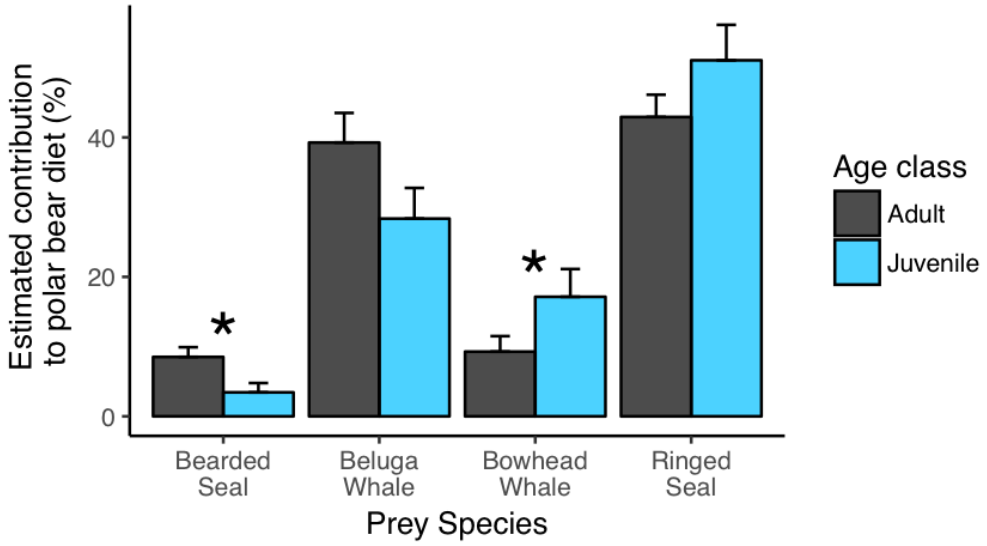

Figure 3. 3 Estimated diet composition of adult (≥5 years old; n = 29) and juvenile (<5 years old; n = 9) polar bears in Viscount Melville Sound from 2012-2014. Significant differences between age classes are indicated by *.

I found no differences between adult male and female consumption of bearded seal (t = -1.21, df = 17.69, p = 0.242), beluga whale (t = 0.89, df = 23.49, p = 0.383), bowhead whale (t = -0.03, df = 20.07, p = 0.977), or ringed seal (Fig. 3.4; t = -0.22, df = 26.31, p = 0.826).

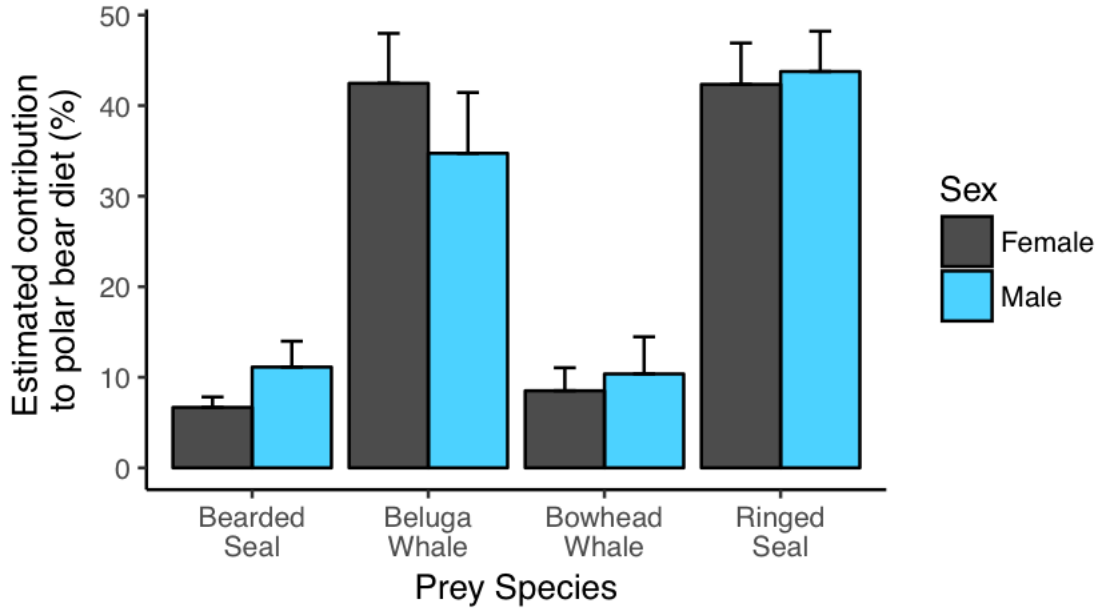

Figure 3. 4 Estimated diet composition of adult females (n = 17) and males (<5 years old; n = 12) polar bears live-captured or harvested in Viscount Melville Sound from 2012-2014.

Because there was no overall significant difference in diet composition between age classes or sexes, all bears in the study were pooled and analyzed for interannual variation. I found no differences in the yearly consumption of bearded seal, bowhead whale, or ringed seal (Fig. 3.5; permutation ANOVA, $p = 0.784$, $p = 0.135$, $p = 0.087$, respectively). However, beluga whale consumption showed interannual variation (permutation ANOVA, $p = 0.042$), with the highest and lowest mean contribution occurring in 2012 and 2014, respectively (Fig. 3.5).

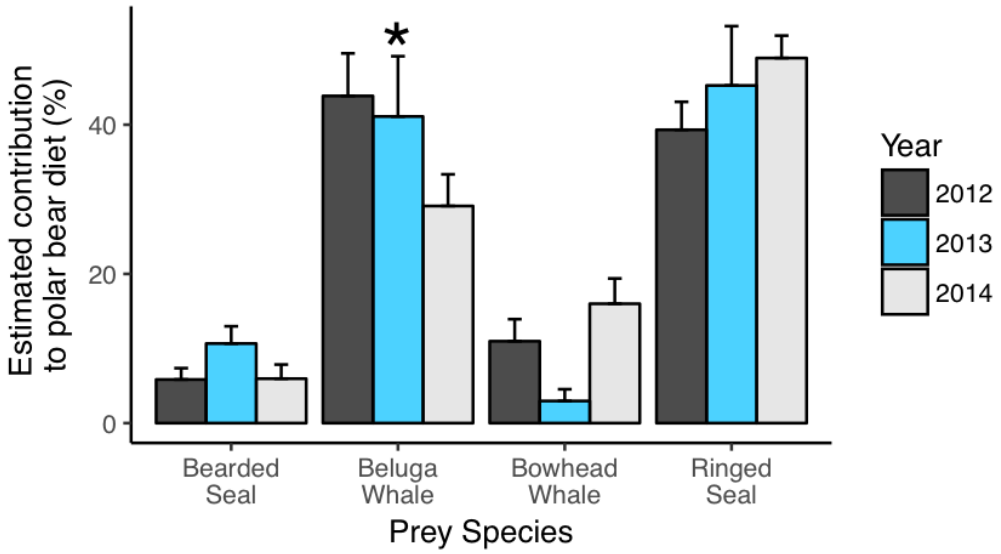

Figure 3. 5 Estimated diet composition of all bears in study for years 2012 (n = 12), 2013 (n = 10), and 2014 (n = 16). Significant differences between years are indicated by *.

Body Condition

Body condition was not correlated with the proportional consumption of any prey type for female polar bears, however there was a non-significant positive trend between bowhead whale consumption and body condition (Fig. 3.6). In male bears, there was a negative correlation between bearded seal consumption and body condition, but no correlations with other prey types and body condition (Fig. 3.6).

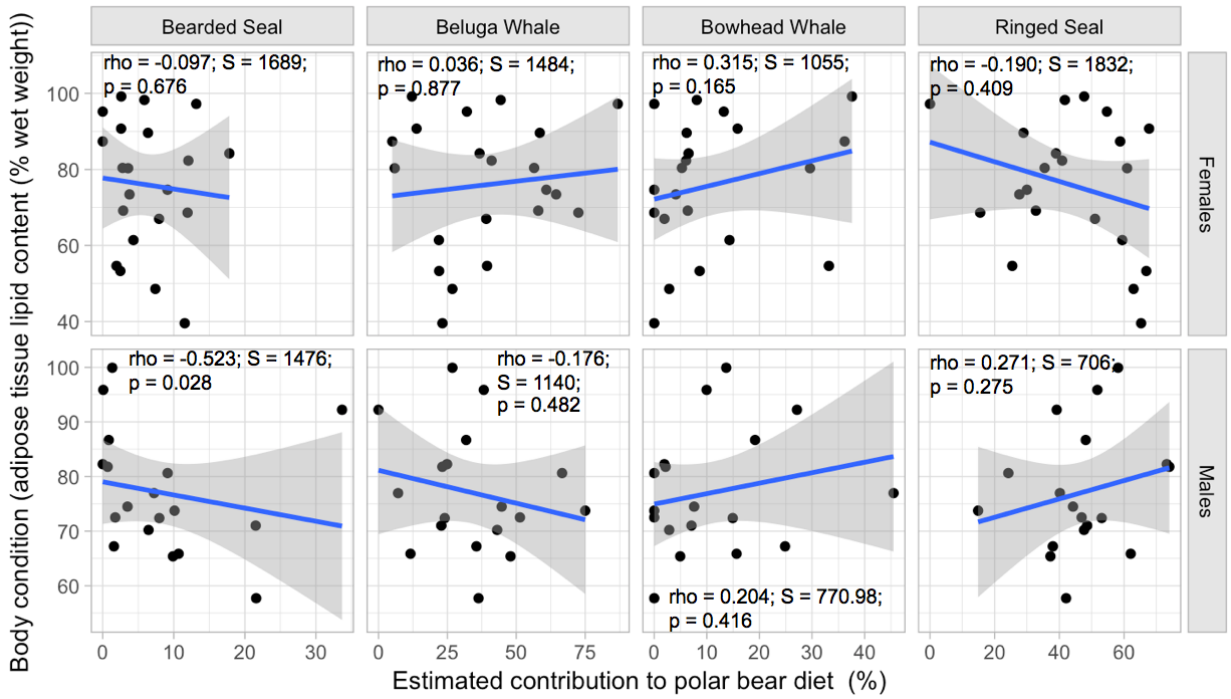

Figure 3. 6 Relationship between diet composition and body condition (adipose tissue lipid content) of polar bears harvested in Viscount Melville Sound from 2012 to 2014. Spearman rank correlation are shown on the figure, with a linear trendline and 95% confidence intervals indicated by grey shading.

Sea Ice Conditions

From 1979 to 2014 the date of spring sea ice retreat varied inter-annually (Fig. 3.7) but did not occur progressively earlier in the year ($R^2 = 0.038$, $F_{1,34} = 2.381$, $p = 0.132$). However, the date of sea ice advance occurred progressively later in the year (Spearman correlation, $R^2 = 0.400$, $p = 0.016$), the duration of the open-water season increased ($R^2 = 0.144$, $F_{1,34} = 6.892$, $p = 0.013$), and the mean summer sea ice concentration declined ($R^2 = 0.235$, $F_{1,34} = 11.74$, $p = 0.002$).

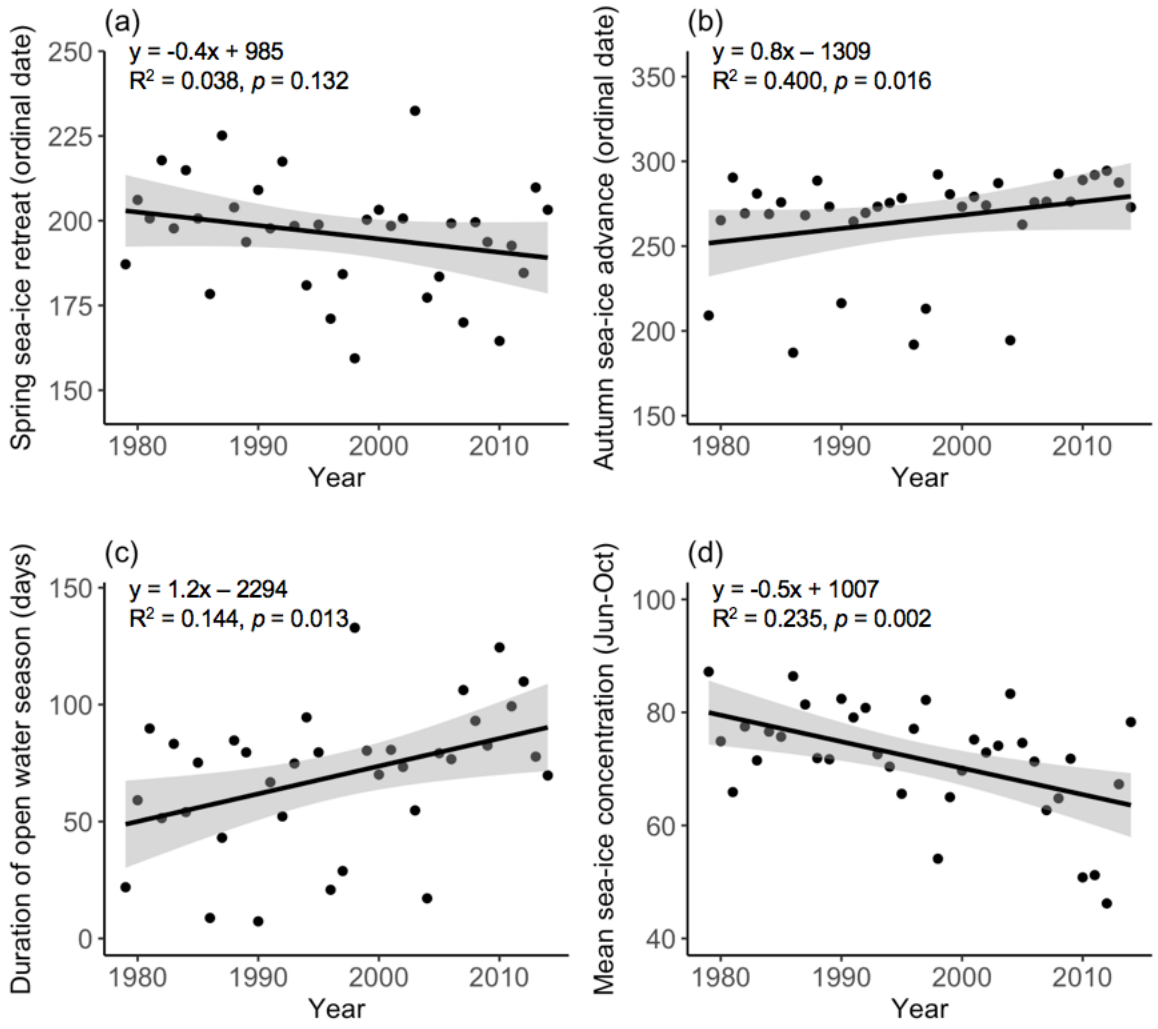

Figure 3. 7 Long-term trends in: a) spring sea ice retreat, b) autumn sea ice advance, c) duration of the summer open-water season, and d) the mean sea ice concentration from 1979 to 2014 within the Viscount Melville Sound polar bear subpopulation boundaries. Statistical results from linear regressions are shown on the figure, with a linear trendline and 95% confidence intervals indicated by grey shading. Data defined by Stern and Laidre (2016).

Because bears were sampled in April/May, the sea ice metrics had not occurred at the time of sample collection, thus, the previous year's sea ice metric was compared to diet and body condition data. Of the three years of sampling polar bears for diet estimation (2012-2014), sea ice retreat occurred earliest in 2012 (Fig. 3.7). Sea ice advance remained within the upper 47.5%

CI in all three years. The duration of the open water season was above the trend line in 2011 and 2012, and below in 2013; the mean sea ice concentration was relatively low in 2011 and 2012, and high in 2013 (Fig. 3.5; comparable to polar bear years 2012, 2013, and 2014 respectively).

As the two dominant prey types, ringed seal and beluga whale followed inverse patterns; when proportional consumption of ringed seal was high, beluga consumption tended to be low, and vice versa (Fig. 3.8). This pattern was evident in both male and female bears, although the relationship between sea ice, body condition, and diet differed between the sexes. In the poor habitat year (i.e., 2012; low summer sea ice concentration, longer open water, earlier break-up, later freeze-up) females consumed little ringed seal and greater beluga whale (in 2013), whereas males exhibited the opposite pattern, consuming proportionately more ringed seal and less beluga than the other two years. Both sexes exhibited their lowest body condition in the poor habitat year. The diets of male and female polar bears were more similar in the other two years of the study, with bears consuming proportionately less beluga with increasing sea ice. Female condition peaked in the intermediate habitat year whereas male condition was highest when sea ice was extensive (e.g., reduced open water, later break-up).

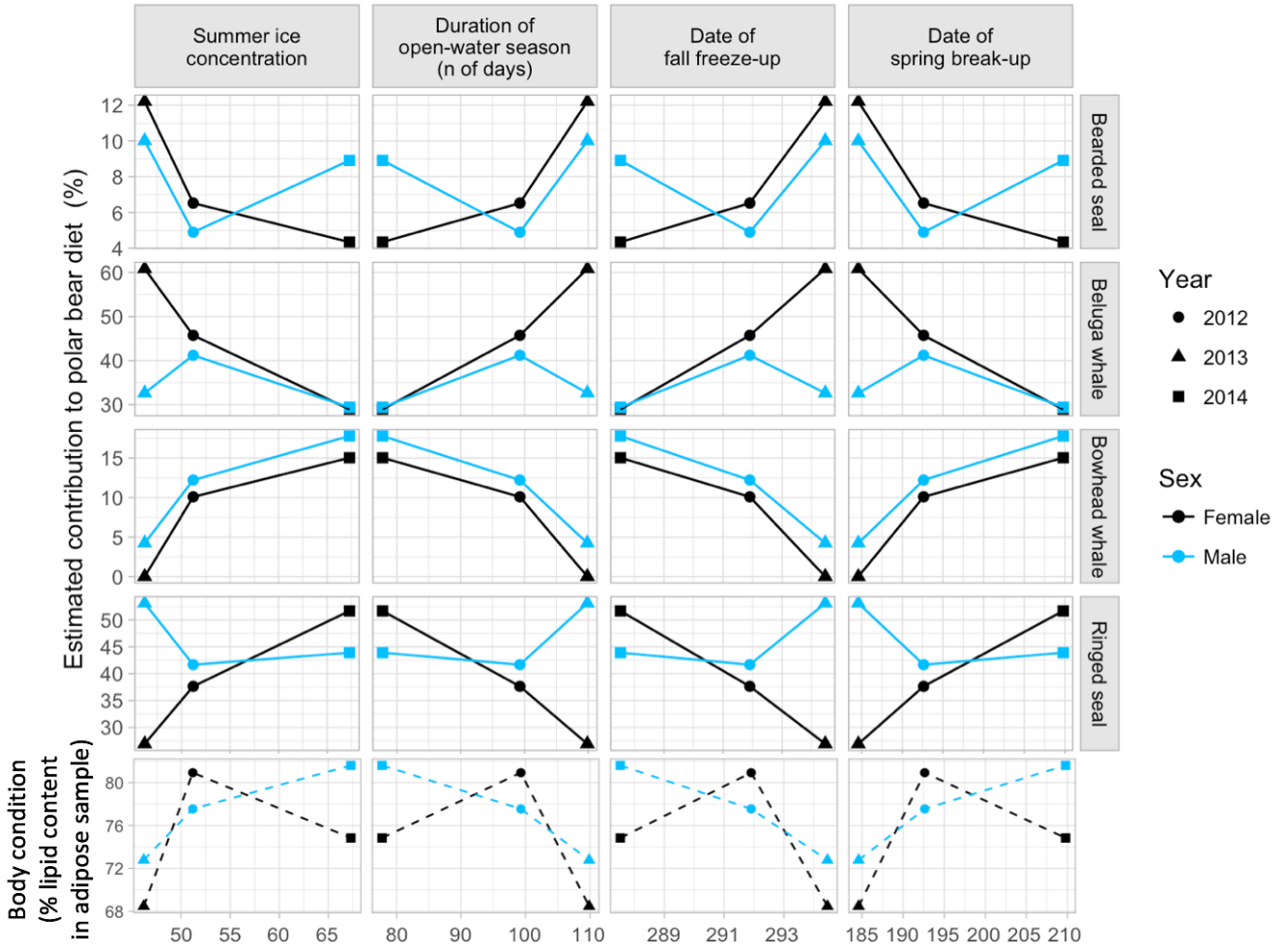

Figure 3. 8 Relationship between sea ice conditions, diet composition (solid line), and body condition (dotted line) of polar bears (separated by sex) sampled in Viscount Melville Sound in 2012-2014. Diet estimates are plotted against the sea ice conditions in the year prior.

Discussion

This study is the first to estimate diet composition of polar bears in Viscount Melville Sound and thus provide insights into the structure and functioning of a marine food web in an area undergoing rapid environmental change. The ecology of polar bears in this subpopulation – including life history patterns, demography, and space use – is poorly understood, but given the rate of sea ice decline in the region, my new data reveal current trophic relationships against

which future ecological changes can be measured. I found that the diets of polar bears in Viscount Melville Sound were dominated by ringed seal (mean = 45.0%), which is comparable to diet estimates from neighboring subpopulations (i.e., Northern Beaufort Sea: mean = 58%; see Chapter 2, Thiemann et al. 2008, Bromaghin et al. 2015; Lancaster Sound: mean = 49%; Galicia et al. 2015). However, I recorded a greater reliance on beluga whale (mean = 36.7%) than documented in any other study (i.e., Thiemann et al. 2008; Bromaghin et al. 2015; Galicia et al. 2015; McKinney et al. 2017; Sciullo et al. 2017). In the adjacent subpopulations of Northern Beaufort Sea to the west and Lancaster Sound to the east, beluga whale consumption was estimated at 18% and 15% respectively; bearded seal was 15% and 24% respectively; bowhead whale was 10% and harp seal was 10%, respectively (Galicia et al. 2015; see Chapter 2).

As predicted, I found adult polar bears were eating proportionately more bearded seal and less bowhead whale than juvenile conspecifics (Fig. 3.3). This is potentially due to the larger body size of adults (Derocher et al. 2005, 2010), which allows them to hunt larger-bodied prey, such as bearded seals, while smaller bears may take advantage of scavenging opportunities at bowhead whale carcasses (Thiemann et al. 2007, 2008a). However, there was no age difference in the proportion of beluga whale consumed (Fig. 3.3). The large size of a beluga whale carcass may support non-aggressive feeding by a number of bears (e.g., Lowry et al. 1987). Not consistent with my predictions, and despite the sexual size dimorphism of polar bears, I found no sex-specific differences in diet composition. The diets of both sexes were dominated by ringed seal and beluga whale.

Sea ice advance occurred progressively later in the year and the duration of the open-water season increased throughout 1979-2014 (Fig. 3.7). Annual sea ice is the primary habitat for polar bears and sea ice declines are expected to negatively affect polar bear foraging success,

body condition, reproduction, and survival (Stirling et al. 1999; Derocher et al. 2004; Regehr et al. 2007; Rode et al. 2010, 2012; Bromaghin et al. 2015; Lunn et al. 2016). Declines in sea ice may also be related to recruitment and survival of ringed seals due to lack of suitable birth lair and haul-out habitat (Ferguson et al. 2005; Harwood et al. 2015; Yurkowski et al. 2016). Historically, heavy sea ice conditions in Viscount Melville Sound were thought to impair biological productivity (Stirling 2002) and lead to lower ringed seal abundance relative to other parts of the Arctic (Kingsley et al. 1985). As multi-year ice in this region is replaced with annual ice, ringed seal productivity may increase, at least in the short term (Derocher et al. 2004). However, the relatively high consumption of beluga whale by polar bears in this study suggests that sea ice changes have not yet resulted in an increase in ringed seal availability.

Beluga whale was the only prey item to differ by year, as consumption of beluga fell in 2014 relative to the two years prior (Fig. 3.5). Since bears were captured in April and May, I compared diet estimates to the prior year's sea ice values (i.e., bear diets in 2014 would be compared to ice conditions in 2013). Relative high beluga estimates in 2012 and 2013 may be explained by relatively longer duration of open water during the summer of 2011 and 2012, whereas 2013 had a shorter summer duration and less beluga consumption, perhaps due to a shorter timeframe for beluga whales to forage in high latitude areas. Additionally, the relatively high ice concentration in the summer of 2013 may have presented a barrier to beluga whale migration to foraging habitats (Hornby et al. 2016) and thus contributed to lower beluga consumption in my 2014 diet estimates. Indeed, Hornby et al. (2016) found that heavy ice conditions in 2013 restricted the habitat use of beluga whales along the Mackenzie Shelf.

Polar bears may have access to beluga whale during ice entrapment events (Lowry et al. 1987; Smith and Sjare 1990; Heide-Jørgensen et al. 2003) or when beluga are in shallow waters

(Smith et al. 1985; Smith and Sjare 1990). Little is known of beluga whale abundance and ecology in Viscount Melville Sound, however polar bears have been observed foraging on beluga whales in July and August near the coast of Somerset Island in Barrow Straight (Smith and Sjare 1990). Because my diet estimates are proportional values, a decline in ringed seal consumption (e.g., because of habitat conditions) could also result in a proportionate increase in beluga whale consumption. Reduced overall foraging success would presumably be evident in the body condition and demographic characteristics of the subpopulation. The relatively low density of polar bears in this subpopulation (E. Richardson, pers. comm. 2017) suggests that the availability of preferred prey is low.

Although the low sample size and short temporal span of my study precluded robust statistical analysis, my data were consistent with linear and non-linear relationships between sea ice habitat and polar bear diet composition and foraging success. For female bears, increasing sea ice duration was associated with higher ringed seal and lower beluga whale consumption, consistent with the role of ringed seal as the primary prey of female polar bears throughout their range. Lower spatiotemporal availability of sea ice was associated with greater consumption of beluga whale, either because ringed seals were less available or beluga density increased, or both (see above). Although ringed seal consumption appeared to increase linearly with sea ice (i.e., date of spring break-up and summer sea ice concentration), female body condition peaked at intermediate sea ice conditions and declined with heavier spring sea ice. Extensive spring sea ice can disrupt ringed seal pupping and past studies have documented declines in both ringed seal and polar bear natality during periods of heavy sea ice in the western Arctic (Stirling 2002).

The foraging habits of male bears appeared to be less sensitive to habitat conditions, as males consumed relatively high levels of both ringed and bearded seal at high and low habitat

conditions. This pattern, combined with less reliance on beluga whale when habitat conditions were poor, is consistent with greater dietary flexibility in males bears, which are able to kill and consume a wider range of prey (e.g., Thiemann et al. 2011) and are not constrained by the presence of cubs. Male foraging success (body condition) showed a more linear and less variable relationship with sea ice than was evident for females, again consistent with greater dietary flexibility and the advantages of absolute larger body size. Moreover, the greater dietary constraint on females (compared to males) suggest female bears are more vulnerable to changes in availability and type of prey populations, and indicates that further research on female polar bear ecology is necessary for proactive population management and conservation.

My results suggest that polar bears in Viscount Melville Sound rely on ringed seal and beluga whale, and to a lesser extent bearded seal and bowhead whale, with age- but not sex-specific differences in diet composition. The effects of climate-driven changes in sea ice are not uniform across the circumpolar distribution of polar bears. The ecological effects of declining sea ice in Viscount Melville Sound remain uncertain. My results provide an important baseline of polar bear foraging and body condition during a period of rapid sea ice decline.

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Chapter 4: Conclusion

Thesis Summary

Polar bears rely on sea ice as a physical substrate to hunt marine mammal prey (Stirling and Derocher 1993). Declining habitat quality due to climate change may result in structural and functional shifts in Arctic marine food webs. Reductions in sea ice are projected to accelerate at rates that differ throughout the circumpolar Arctic. Declines in ice may be linked to recorded declines in polar bear reproduction and survival (Regehr et al. 2007; Rode et al. 2010, 2012), presumably by reductions in foraging opportunities. In this thesis, I quantified the diets of polar bears in three subpopulations of the western Canadian Arctic: Southern Beaufort Sea (dramatic sea ice loss and population instability; Bromaghin et al. 2015), Northern Beaufort Sea (high-latitude region with comparatively little change in sea ice; Stern and Laidre 2016), and Viscount Melville Sound (largely unknown ecosystem). In addition to quantifying polar bear diets, I characterized body condition and sea ice conditions, and compared the three to understand the impacts of declining sea ice conditions on polar bear ecology. The results from this thesis fill important gaps in the understanding of Arctic food web ecology by providing insights on the effects of ice loss on diet and body condition, and by establishing baseline data against which future ecological changes can be measured.

The biggest driver of diet was location (specifically longitude) of polar bears at harvest or capture. In the Beaufort Sea, bears were eating proportionately more bearded seal and less ringed seal in the west, and vice versa in the east of the study area. However, my diet estimations for polar bears in Viscount Melville Sound record the heaviest reliance on beluga whale consumption than any other studied subpopulation, potentially suggesting low ringed seal availability. Long-term temporal trends were investigated in Northern and Southern Beaufort Sea subpopulations but not Viscount Melville Sound due to limitations on study duration in Viscount

Melville Sound. Long-term studies provide insights on ecological trends, however, short-term studies are important for establishing baseline information. In the Northern Beaufort Sea subpopulation, I found an inverse relationship between amount of ringed seal and beluga whale in polar bear diet. For bears in the Southern Beaufort Sea, I binned diet data in three time periods, however I did not find a directional trend consistent with Bromaghin et al.'s (2015) hypothesis that low survival in 2004-2006 may have been due to low prey abundance or limited prey access for any specific species. Furthermore, I found sex differences in diet in the Northern and Southern Beaufort Sea subpopulations, but not Viscount Melville Sound. However, in all three subpopulations I found age differences, specifically with males eating more bearded seal with age.

Previous studies have found reductions in sea ice to be linked to declines in polar bear body condition, reproduction, survival, and abundance. However, the mechanisms of these impacts are not well understood. My thesis provides insights into the relationship between sea ice, diet, and body condition and the potential effects of rapid reductions in sea ice. Previous studies have suggested sea ice conditions limit beluga whale movement, and my results provide support that later sea ice break-up may lead to entrapment events, providing an important food source for polar bears. Furthermore, I found a positive correlation between ringed seal consumption and body condition (as inferred by adipose tissue lipid content) of female bears, suggesting ringed seals are the preferred prey and their availability may have the largest effect on body condition.

Conservation Implications

Polar bear foraging ecology varies spatially: both across regions in this thesis, and across other studied subpopulations, presumably in response to variable prey availability and habitat quality. This study provides insight for conservation by quantifying intraspecific diet variation, how changes in ice impact diet, and by establishing important baseline dietary information for bears in Viscount Melville Sound to be monitored in the future. While polar bear movement is not restricted by subpopulation boundaries, information on polar bear foraging ecology within and across subpopulations is important for assessing conservation status and informing local management decisions. Ultimately, my results have contributed to an improved understanding of the mechanistic relationships between habitat conditions and polar bear foraging ecology, which can be used to make inferences about the demographic responses of polar bear subpopulations to future sea ice declines.

Arctic research is often restricted by financial and logistic limitations. This study used samples provided from subsistence harvest and thus is a result of Hunter and Trapper Organization efforts. Insights from this study would have otherwise not been possible, emphasizing the importance of continuing community-based programs.

Future Research

This thesis provides diet and body condition data on polar bears in relation to sea ice conditions in Viscount Melville Sound, and additionally investigated temporal trends of bears in the Northern and Southern Beaufort Sea subpopulations. While my thesis contributes towards a better understanding of Arctic marine food web ecology in the Western Canadian Arctic, continued monitoring of these subpopulations could inform how projected declines in sea ice may alter polar bear foraging ecology. Particularly as sea ice regime changes in Viscount

Melville Sound, presumably shifting prey species abundance, it would be interesting to monitor concurrent changes in polar bear diet and body condition to my baseline results provided in Chapter 3. Furthermore, it is important to continue Beaufort Sea monitoring, both in the Amundsen Gulf where ringed seal productivity is comparatively high, and also in the Southern Beaufort Sea subpopulation where sea ice is declining at a relatively rapid rate. More importantly, this thesis sets the stage for further interesting research questions, for example, how foraging ecology is influenced by predator-prey abundance and space use.

Understanding polar bear prey selection could be accomplished by conducting prey abundance surveys at multiple times of year to understand local trends in availability. Inter-species studies incorporating body condition of prey species (i.e., from ringed seal monitoring in the Amundsen Gulf) to polar bear diet analyses may be useful to address questions about how polar bears use different prey types in years of high and low body condition (and natality) in the prey. Additionally, a temporal analysis of multiple species abundances in relation to sea ice allow further understanding of energy flow through the Arctic marine food web: for example, conducting surveys on marine mammal prey (i.e., potentially fluctuations between Arctic cod, capelin, and sand lance), in unison with analysing pinniped, cetacean, and polar bear diet could provide insights on how 1) shifts in fish species abundance influence higher food web species diet and body condition and 2) how sea ice conditions in individual years influence the foraging ecology and abundance of species at different trophic levels. The results from this thesis on the relationship between sea ice and polar bear diet could serve as an important baseline for which future studies can be based.

There is currently limited understanding of marine mammal abundance in the Viscount Melville Sound region. Chapter 3 reveals the diet composition and body condition of polar bears,

however, little is known about local habitat use by beluga and bowhead whales, bearded seals, or ringed seals. A quantitative estimate of prey abundance, including seasonal movements and fluctuations in local species, could provide valuable insight into the ecology of the Arctic marine environments, and is important to further establish baseline information on habitat use in a region expected to undergo further sea ice reductions.

In conclusion, this thesis examined the relationship between sea ice, diet, and body condition of polar bears across the western Canadian Arctic over a period of sea ice decline. My results detail the variation in foraging ecology between demographic groups, spatial regions, and time, and highlight the impacts of sea ice regime on foraging and body condition. Additionally, I provide the first diet and body condition estimates for polar bears in Viscount Melville Sound, a largely unknown, high-latitude region. These results provide information valuable for assessing how projected sea ice declines may continue to affect polar bear foraging ecology and body condition.

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